Life history and mating system of the brown thornbill

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Declaration

The research described in this thesis is my own original work and no part has been submitted for a previous degree. Chapter 2, chapter 4, and chapter 5 are co-authored by Andrew Cockburn who contributed discussion, together with facilities and financial support for the DNA fingerprinting. Chapter 5 is also co-authored by Anne Peters who assisted with the DNA fingerprinting. However, I am the principal contributor to all aspects of the work.

Signed

David J. Green

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Abstract

This thesis describes the life history and mating system of the brown thornbill (*Acanthiza pusilla*, Acanthizidae). I carried out the study on a population of approximately 30 pairs in and adjacent to the Australian National Botanic Garden, Canberra, Australia between 1995 and 1999.

Brown thornbills bred exclusively in pairs although cooperative breeding is the ancestral trait in this family. Pairs defended small (ca. 2 ha) territories year round. Females laid up to three clutches (98% contained 3 eggs), but rarely fledged more than one brood during a breeding season that extended from late July (mid-winter) to December (early summer). Pairs produced an average of 1.57 fledglings and 1.03 independent young per year. Annual reproductive success of individual pairs was, however, strongly correlated with male age. Male performance improved during two stages of the breeding cycle: first-year males were less likely to fledge young than those aged two or more, while both first and second-year males were less successful at raising fledglings to independence than males older than two. Both adult males and adult females had relatively high annual survival rates (ca. 63%). The life history and demography of the brown thornbill was no different to that of cooperative species from the Acanthizidae. Pair-breeding in brown thornbills is therefore unlikely to have evolved in response to changes in life history or demography.

To evaluate whether pair-breeding has evolved in response to the relaxation of ecological constraints on dispersal I examined dispersal strategies and recruitment in brown thornbills. Juvenile brown thornbills either dispersed at the end of the breeding season or delayed dispersal and remained on their natal territory into the autumn and winter. Juvenile males were far more likely to delay dispersal than females. Juveniles that delayed dispersal suffered little mortality and were four times more likely to gain a breeding vacancy in the local breeding population than juveniles that dispersed at the end of the breeding season. Juveniles from both pair-breeding and cooperative species therefore appear to benefit from prolonged natal

philopatry. However, only half the pairs of brown thornbills which produced independent young retained offspring on their territory. Constraints on delayed dispersal were found to limit opportunities for juveniles to help their parents and appear to be a major factor leading to the evolution of pair-breeding in the brown thornbill.

Brown thornbills were genetically as well as socially monogamous. DNA fingerprinting revealed that extra-pair males sired only 6.2% of 178 offspring (11.9 % of 67 broods). Male brown thornbills ensured paternity in their own broods by guarding their mates closely when they were fertile which enabled them to detect and then evict rival males before were able to approach the female. Females did not attempt to escape male guarding, but given the opportunity would solicit copulations from intruding males. Males that were either small and/or breeding for the first time were more likely to be cuckolded than larger and older males.

Female brown thornbills adjusted the sex ratio of their offspring in response to the costs and benefits associated with raising sons and daughters. Female thornbills in new pairs produced female-biased broods while females in established pairs produced male-biased broods. I evaluated the fitness consequences of this pattern by manipulating the sex ratio of broods provisioned by new and established pairs. Although sons have higher energy requirements than daughters, the increased costs of raising sons are confined to females in new pairs. The costs of raising sons differ for females in new and established pairs because males in new pairs provision at a lower rate than males in established pairs and male thornbills do not adjust their feeding rates in response to the sex ratio of the brood. Females in new pairs with male-biased broods are therefore forced to provision at a higher rate and yet still produce nestlings that are in relatively poor condition and consequently unlikely to obtain a breeding vacancy. Female brown thornbills therefore obtain fitness benefits from adjusting the sex ratio of their offspring in response to the level of resources provided by their partner.

Table of Contents

Chapter 1.

General Introduction

"monogamy, in birds and man, tends to be dressed in drab colours, but is far more frequent than the exotic alternatives" David Lack 1968

David Lack (1968) pointed out that the majority (> 90%) of bird species breed in pairs. The prevalence of pair-breeding in birds has led to the widespread assumption that evolution inevitably proceeds from pair-breeding to alternative, less common, avian breeding systems. Consequently, ornithologists have invested considerable effort to develop models that account for the evolution of polygyny (eg. Orians 1969, Emlen and Oring 1979), lek or display-site promiscuity (eg. Bradbury 1981, Bradbury and Gibson 1983, Beehler and Foster 1988), and cooperative breeding (eg. Emlen 1982, Stacey and Ligon 1991). These models emphasise the role of resources for females, availability of mates for males, and the availability of breeding vacancies to young birds in determining avian social systems.

Phylogenetic studies conducted over the last decade have illustrated that avian mating systems are not distributed randomly among taxa (Russell 1989, Edwards and Naeem 1993, Ketterson and Nolan 1994), which suggests that phylogenetic history may also play an important role in explaining variation in avian mating systems. For example, there is a strong phylogenetic component to the distribution of cooperative breeding in contemporary birds (Russell 1989). Cooperative breeding is relatively common in the Corvida, the group of passerines that originated and radiated within Australia (approximately 25% of species world-wide), but rare in the other major radiations of passerine birds (Tyrannides: < 1%; Passerida: approximately 2%; Cockburn 1996).

Studies that have used well-resolved phylogenies to examine the distribution of cooperative breeding in groups within the Corvida also provide compelling evidence that evolution does not necessarily proceed in just one direction. For example, Christidis and Schodde (1993) showed that in the meliphagine honeyeaters cooperative breeding has evolved from pair-breeding on several occasions. In contrast, Peterson and Burt (1992) showed that pair breeding evolved from cooperative breeding in a single clade of *Aphelocoma* jays. More recently, Nicholls

et al. (2000) have demonstrated that cooperative breeding is likely to be the ancestral condition in the Acanthizidae, and that pair-breeding has evolved independently at least four times in this family; twice within the genus *Acanthiza*, once within the genus *Gerygone* and once within the genus *Sericornis*. These studies demonstrate that it is necessary to be wary of assuming that cooperative breeding in the Corvida has evolved in response to contemporary conditions since any phylogenetic inertia will tend to result in the retention of cooperative breeding in inappropriate habitats. Studies focussed on examining what factors influence the evolution of pair-breeding in families where it is known to be a derived trait may shed more light on the evolution of breeding systems in the Corvida.

The Acanthizidae is a family that provides an excellent opportunity to investigate factors that influence the evolution of pair-breeding in the Corvida. This family provides a suitable model for the study of avian social evolution for three reasons. First, a detailed phylogeny has been produced for two of the large genera within the family (*Acanthiza*, Nicholls et al. 2000; *Sericornis*, Christidis et al. 1988). Second, the family includes pair and cooperatively breeding species that are found in a variety of habitats throughout Australia. Third, four species from the Acanthizidae that breed cooperatively (yellow-rumped thornbill *Acanthiza chrysorrhoa*, buff-rumped thornbill *A. reguloides*, speckled warbler, *Chthonicola sagittata*, and white-browed scrubwren *Sericornis frontalis*) are currently the focus of long term field studies in Canberra, Australia. Consequently, detailed study of one or more pair-breeding species will allow examination of the role that ecology, demography, and life history play in the evolution of pair-breeding in the Acanthizidae.

Pair-breeding and cooperative breeding in birds.

Despite the prevalence of pair-breeding in birds relatively little is known about factors that promote the evolution and maintenance of this mating system. Pair-breeding is usually argued to have evolved and be maintained because biparental care is essential for the production of independent offspring (Lack 1968),

and/or because male birds are unable to obtain extra mates (Emlen and Oring 1977, Wittenberger and Tilson 1980).

Cooperative breeding in birds has, in stark contrast, been the subject of considerable research over the last 30 years (for recent reviews see Koenig et al. 1992, Cockburn 1998). The most widely accepted models which attempt to account for the occurrence of cooperative breeding emphasise the importance of ecological constraints on independent breeding. Young birds are argued to defer dispersal either because of a shortage of vacant breeding territories and a low probability that dispersal leads to independent reproduction (habitat constraint models: Emlen 1982, Brown 1987) or because habitat is so variable that it pays to remain on their natal territory and wait for a high quality territory rather than attempt to breed on a poor quality one (benefits of philopatry model: Stacey and Ligon 1991). These models have received considerable support from detailed studies of individual species. Studies have both identified constraints that prevent independent reproduction (eg. a shortage of territory vacancies, Woolfenden and Fitzpatrick 1984; high dispersal costs, Ligon and Ligon 1990; a shortage of breeding partners, Pruett-Jones and Lewis 1990) and been able to demonstrate that benefits of natal philopatry may lead to delayed dispersal even when habitat is not saturated (eg. Komdeur 1992). However, these models are not able to provide an explanation for why some species breed cooperatively while others do not (Heinsohn et al. 1990, Cockburn 1996).

Comparative studies provide an alternative approach that may be used to identify circumstances that favour cooperative breeding in birds. The comparative analyses conducted by Arnold and Owens (1998, 1999) are the most sophisticated to date. Arnold and Owens (1998, 1999) concluded that the key factor that predisposes certain avian lineages to cooperative breeding is low annual mortality, but that two ecological factors, warm winters and a limited temperature range, enable species to be sedentary and facilitate cooperation within these predisposed lineages. Cockburn (1996) also argued that low annual mortality may account for the prevalence of cooperative breeding in the Corvida, but observed that the main ecological pattern in the dispersion of cooperative breeding in this group is the tendency for non-

cooperative species to be found in dense, visually occluded habitat. He suggested that dominant birds may have more difficulty maintaining control over group members in such habitats, and that increased reproductive conflict may make it too costly for adults to allow juveniles to remain on their natal territory.

In this thesis I examine the life history of the brown thornbill *Acanthiza pusilla* and evaluate the arguments that have been invoked to explain the distribution of pair-breeding and cooperative breeding in birds.

Structure of thesis

Brown thornbills are thought to breed exclusively in pairs (Bell and Ford 1886). However, quantitative data on their breeding biology is limited. **In chapter 2**, I describe the basic breeding biology, life history and demography of the brown thornbill using data collected over four seasons. I compare the life-history and demography of pair-breeding and cooperatively breeding species within the Acanthizidae (Schodde and Mason 1999; formerly classified as sub-family Acanthizinae within the Pardalotidae, Christidis and Boles 1994), and evaluate whether differences in life-history and demography are likely to explain variation in breeding systems within this family.

The longevity of species within the Corvida has been argued to be a major factor responsible for the prevalence of cooperative breeding in the Corvida (Cockburn 1996). Brown thornbills, despite their small size (ca 7g), can be extremely long lived (up to 17 years , Baker et al. 1999). **In chapter 3**, I examine how age influences the reproductive performance of male and female brown thornbills. In addition, I evaluate whether pair-bond duration has an effect on reproductive success after controlling for the age of the pair.

The ecological constraints models developed to explain variation in avian breeding systems suggest that pair-breeding may evolve from cooperative breeding if the costs associated with dispersal to suitable habitat are reduced or there are few benefits to juveniles associated with prolonged natal philopatry. Alternatively, pair-breeding may be expected to evolve, even when offspring benefit from prolonged

natal philopatry, if the costs to adults of juvenile retention are intolerable (Cockburn 1996). **In chapter 4**, I describe patterns of post-fledging care, dispersal, and recruitment in four cohorts of brown thornbills. I examine what prompts dispersal by juvenile thornbills, and investigate how the timing of dispersal affects recruitment.

Juveniles that remain on their natal territory may subsequently compete with parents for opportunities to reproduce. For example, in the white-browed scrubwren sons that remain on their natal territory may compete with their fathers over paternity of young produced by unrelated females (Whittingham et al. 1997). Conflict over paternity may be sufficient to result in selection for pair-breeding in lineages where fathers are unable to exert sufficient control over sons (Cockburn 1996). **In chapter 5**, to enable patterns of paternity in *Acanthiza* species which breed in groups to be compared with those which breed in pairs, I use DNA-fingerprinting to determine the level of extra-pair paternity in brown thornbills. I also investigate the role of female choice, male-male competition, and conflict between pair members in determining paternity.

Female brown thornbills provision young with the assistance of their mate, but unlike cooperative species in the *Acanthiza* are not able to obtain additional assistance from helpers. **In chapter 6**, I examine sex ratio variation in brown thornbills, and show that females obtain fitness benefits from adjusting the sex ratio of their brood in response to the level of parental care provided by their mate.

Finally, **in chapter 7,** I evaluate explanations for the evolution of pair-breeding in the Acanthizidae, outline some of the unresolved issues arising from my research, and suggest further work which might help resolve them.

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Chapter 2

Life history and demography of an uncooperative Australian passerine, the brown thornbill

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Abstract

The *Acanthiza* may be important in understanding the evolution of avian mating systems because while brown thornbills *Acanthiza pusilla* are thought to breed only in pairs, a recent phylogenetic analysis suggests that cooperative breeding is the ancestral trait within this genus. We provide a detailed account of the breeding biology of the brown thornbill, confirm that they breed exclusively in pairs, and compare their population demography with what is known for other members of the Acanthizidae. We found that brown thornbills produced small clutches (3 eggs) with a two-day laying interval, had a long incubation period (declining from 19 to 16 days through the season), and had a long breeding season (4.0 months) that allowed females to occasionally raise two successful broods. Brown thornbills, in our study, produced an average of 1.57 fledglings per pair and had relatively high annual survival rates (ca. 63%). We found no evidence to suggest that the evolution of pair-breeding within the Acanthizidae is associated with a reduction in annual survival rates, a short breeding season with reduced productivity, or high levels of predation post-fledging. Since there also appear to be no ecological correlates with mating system in the Acanthizidae we suggest that examination of reproductive conflict between parents and young may shed light on the evolution of pair-breeding in this family.

Introduction

Studies of avian mating systems have recently begun to use a comparative approach to examine the life history traits of pair-breeding and cooperatively breeding birds (Poiani and Jermin 1994, Poiani and Pagel 1997, Arnold and Owens 1998). Arnold and Owens (1998) argue that extremely low adult mortality may predispose some avian families to breed cooperatively. This approach has been galvanised by the detailed phylogeny available for birds (Sibley and Ahlquist 1990), but is compromised by the lack of detailed data on the breeding biology of birds from the southern hemisphere (Martin 1996).

The Corvida, an ancient clade of passerines which evolved and radiated mostly within Australia, play an important role in comparative analyses of life history traits because cooperative breeding is much more prevalent in the Corvida than the Passerida, the clade to which most well studied species belong (Russell 1989, Cockburn 1996). The Australian endemics are thought to possess a suite of life-history traits resulting in long, slow reproduction, but current analyses do not support the view that cooperative Corvida in Australia have different demography from non-cooperative taxa (Ford 1989, Rowley and Russell 1991, Poiani and Jermin 1994).

The Acanthizidae are a speciose family from the Corvida that contains both pair-breeding and cooperatively breeding members. They are known for their longevity, small clutch sizes, long incubation periods, and prolonged breeding seasons (Woinarski 1985, Yom-Tov 1987, Rowley and Russell 1991, Yom-Tov et al. 1992, Ricklefs 1993). Nevertheless only a few of the 45 species of Acanthizidae resident in Australia have been studied in detail, eg. *Acanthiza pusilla* and *A. reguloides* (Bell and Ford 1986), *A. chrysorrhoa* (Ford 1963), *Sericornis frontalis* (Ambrose and Davies 1989, Magrath et al. 2000). Even for these species, quantitative data often do not cover the whole breeding season and little is known about seasonal effects on reproduction.

We describe the breeding biology of the brown thornbill, *Acanthiza pusilla,* a small (ca. 7g) insectivore common in forested areas of south-eastern Australia.

Brown thornbills are one of 12 *Acanthiza* species endemic to Australia. This genus may be important in understanding the evolution of avian mating systems because while brown thornbills are thought to breed only in pairs (Bell and Ford 1986), a recent phylogenetic analysis suggests that cooperative breeding is the ancestral trait within the *Acanthiza* (Nicholls et al. 2000).

Specifically, we aim: (1) to provide a detailed account of the breeding biology of a small, sedentary, Australian endemic; and (2) compare the population demography of this pair-dwelling member of the Acanthizidae with what is known for other species within the family that breed cooperatively.

Methods

Study population

We studied a colour-banded population of brown thornbills in and adjacent to the Australian National Botanic Garden in Canberra, Australia, from 1995 to 1999. The vegetation in the Botanic Gardens consists of both plantations of Australian native trees and shrubs, and natural woodland which is contiguous with a large area of dry sclerophyll forest (*Eucalyptus rossii, E. mannifera, E. macrorhyncha*) in Black Mountain Nature Reserve. We followed the fate of 15-32 pairs per year, monitoring the entire population resident in the 80 hectare study area between 1996 and 1999.

General methods

We monitored the study population throughout the year. During the non-breeding season (January to June) we visited the study area at least once a month to census pairs, document survival, and identify when new birds entered the population. During the breeding season (July to December) each pair was monitored at least three times a week to document reproductive attempts. The location of birds during territorial disputes was used to determine territory boundaries.

Most birds monitored during the breeding season were uniquely colour banded (> 95 % each year). Adult birds were banded using a numbered Australian Bird and Bat Banding Scheme aluminium band and three plastic colour bands (n =

136). The four bands weighed a total of 0.09 g, approximately 1% of adult body mass, and did not appear to alter the behaviour of the birds in any way. We weighed birds to the nearest 0.1 g using Pesola spring balances whenever they were caught. We also measured wing and tail length to the nearest 1 mm using a stainless steel ruler, and tarsus length and head-bill distance to the nearest 0.05 mm using dial calipers.

Survival of banded individuals was measured from the start of one breeding season (1 August) until the beginning of the next. We assumed birds had died if, after being a member of a breeding pair, they disappeared and were not seen again despite searching the study area and all suitable habitat within 0.5 km of the territory.

We found nests by watching females building nests (n = 126), following females back to their nests during incubation (n = 43), or by watching adults feed nestlings (n = 4). The majority of nests (ca. 78%) were built within a metre of the ground (mean height = 80 cm; range = 10 cm - 7 m). The progress of a nesting attempt was monitored by checking nests at 2-3 day intervals. In 1995 and 1996 we determined laying intervals by checking nests daily from the laying of the first egg until a clutch was completed. In 1997 and 1998 we only checked nests sufficiently to determine the date that the first egg was laid. If we did not find the nest until after laying we estimated the clutch initiation date from the hatching date and regression of incubation period on clutch initiation date. For the few nests that were too high to be accessible (n = 7) we estimated the clutch initiation date by backdating from the time that females were first seen incubating or adults were first seen feeding nestlings.

We defined the incubation period as the interval between the laying of the last egg and the hatching of the last chick. We determined the date of hatching from daily visits to the nest after the female had been incubating for approximately 14 days combined with the appearance and size of nestlings. We banded the nestlings when 7-10 days old. All nestlings were weighed when banding took place and, in 1997 and 1998, were also weighed when 11-12 days old.

We calculated the nestling period as the interval between the hatching of the last chick and fledging of the last chick. We assessed the success of a nesting attempt by monitoring nests every 2-3 days for the first two weeks of incubation, and subsequently used daily visits to determine the date broods fledged. For breeding attempts that failed, nests were assumed to have failed on the day after the nest was last known to be active.

The survival of fledglings was determined by weekly censuses conducted between two and eight weeks after fledging. The duration of parental care was evaluated from 15-30 minute observations on individual fledglings conducted at the same time as the censuses.

Sexing individuals

Brown thornbills can not be sexed on the basis of their plumage but only females are thought to build nests and incubate eggs. We initially sexed birds behaviourally but subsequently used a simple PCR-based molecular technique to confirm their gender (see Griffiths et al. 1998 for details of the method).

Statistical analysis

We used a modelling approach in statistical analysis. Our data contained pairs that were represented several times, as pairs could have multiple nesting attempts in any one year and be present for more than one year of the study. We therefore analysed our breeding data using mixed models incorporating both random and fixed effects, where 'Pair' was included as a random factor in all models (Bennington and Thayne 1994). A new pair was considered to have formed when either member was replaced following a death or divorce.

We fitted separate models using eight dependent variables. The date that a pair initiated their first and their last clutch was used to examine the timing of breeding. We also examined the likelihood that a pair would re-nest following a successful or failed attempt, and the time interval between breeding attempts. The success of each nesting attempt was examined at three stages: hatching (for all

clutches that were initiated), fledging (for all clutches that hatched), and post-fledging (for all broods that fledged).

We used four explanatory variables in our mixed models: year, month, date, and territory type (watered plantation or native woodland). A final model was selected by sequentially dropping non-significant interactions and then non-significant main effects, until only significant terms remained. To avoid any confounding order effects any term that was close to significant ($p < 0.2$) was re-evaluated by adding and dropping it from the final model. We only report main effects or interactions from a model where they are significant ($p < 0.05$), a trend ($p < 0.1$), or it is of biological importance to find a non-significant result. In the case of non-significant effects the statistics refer to the results of the final model plus the non-significant term.

Models were fitted using Genstat v. 5.3.2 (Genstat 1993). Continuous dependent variables were analysed using the restricted maximum likelihood (REML) procedure while binary dependent variables were analysed using the generalized linear mixed model (GLMM) procedure.

Analyses were restricted to pairs where we documented all nesting attempts during the breeding season even if they failed during incubation. Sample sizes vary between analyses because nests were found, and failed, at different times during the breeding cycle. We also excluded 14 pairs whose nests were protected during an experiment in 1998 from analyses of hatching, fledging success.

Survival data were analysed using Cox's proportional hazards model as implemented in JMP v. 3 (SAS Institute 1994). For other analyses, where birds were only represented once, we used conventional least squares statistics. In all analyses residual plots and normal probability plots were examined for unequal variance and deviations from normality among residuals. We applied appropriate transformations if necessary. Means are presented with standard errors unless otherwise stated.

Results

Adult size

Male thornbills were significantly larger and heavier than females but there was overlap in all morphological measures (Table 1). Female thornbills could, however, be sexed accurately on the basis of nest-building and incubation behaviour as the molecular sexing technique always confirmed the gender of birds sexed using behavioural cues (n = 58 pairs).

Annual survival

Adult survival of brown thornbills varied between a high of 85% in 1995 and a low of 37% in 1998 (year effect: $\chi^2_3 = 34.3$, $p < 0.001$). Overall, the survival of male and female thornbills was equal, although males showed more extreme year to year variation (gender effect: $\chi^2_1 = 0.01$, $p > 0.9$, Table 2). Individuals in artificially watered territories were no more likely to survive than those in natural woodlands (watered plantation 62%, natural woodland 64%; $\chi^2_1 = 0.73$, $p > 0.25$). Mortality was observed at all times of the year, however mortality was high during the autumn of 1997, and extreme during September and October in 1998 (Fig. 1).

Social organisation

Brown thornbills maintained territories, ranging in size from 0.4 to 3.1 hectares, throughout the year. Pairs living in artificially watered plantations had significantly smaller territories than pairs living in natural woodland (1997 territories: plantations 1.3 ± 0.1 ha, n = 15; woodland 2.1 ± 0.1 ha, n = 14; t-test, t = 3.87, $p < 0.001$). Territory boundaries did not change significantly from year to year. Brown thornbills bred only in pairs (n = 105 pair-years). A single independent young sometimes remained with their parents in the natal territory through the autumn and early winter (n = 26 cases) but always dispersed or established a territory adjacent to their parents by the start of the breeding season. The late dispersing young were almost always male (25 of 26 juveniles; Chapter 4). We never observed

Table 1. Comparison of mass and linear morphological measurements for male and female brown thornbills.

	Male		Female		t-test
	mean ± S.D.	range	mean ± S.D.	range	
Mass (g)	7.3 ± 0.4	6.6 - 8.0	6.4 ± 0.4	5.7 - 7.1	14.3*
Head-bill (mm)	26.9 ± 0.6	26.1 - 27.7	25.9 ± 0.4	25.0 - 27.1	10.6*
Tarsus (mm)	20.5 ± 0.6	19.4 - 21.3	19.7 ± 0.5	18.6 - 20.4	7.7*
Wing (mm)	52.0 ± 1.5	49 - 56	49.5 ± 1.5	45 - 52	10.0*
Tail (mm)	49.1 ± 2.5	45 - 56	47.2 ± 2.1	44 - 51	4.9*
N	71		65		

* $p < 0.0001$

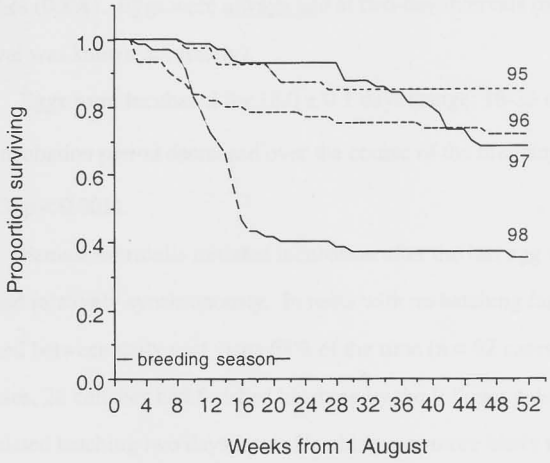


Figure 1. Year-specific survival for colour-banded adult brown thornbills resident in the study area. Sample sizes for 1995 through 1998 are 39, 60, 63, and 65 respectively.

young from previous years or early broods assist their parents raise nestlings or fledglings produced by subsequent nesting attempts.

Breeding biology

Brown thornbills typically laid three-egg clutches (97.6%, n = 126 clutches found before egg-laying), but occasionally produced two-egg (1.6%) or four-egg clutches (0.8%). Eggs were always laid at two-day intervals (n = 23 cases where the interval was known accurately).

Eggs were incubated for 18.0 ± 0.1 days (range: 16-23 days, n = 92 clutches). The incubation period decreased over the course of the breeding season (Fig. 2a; $\chi^2_1 = 29.3$, $p < 0.001$).

Female thornbills initiated incubation after the last egg was laid and clutches hatched relatively synchronously. In nests with no hatching failure the entire clutch hatched between daily nest visits 68% of the time (n = 92 cases). Of the remaining 29 cases, 28 clutches had finished hatching by the following day, while one clutch completed hatching two days later. Hatching was more likely to be totally synchronous early in the season (date effect: $\chi^2_1 = 4.2$, $p < 0.05$).

Nestlings remained in the nest for 16.5 ± 0.8 days (range: 15-18 days, n = 63 broods). The nestling period declined over the breeding season (Fig. 2b; $\chi^2_1 = 14.7$, $p < 0.001$).

Thornbills started to initiate clutches between July and October, with 73% of first clutches being initiated in August and September. Pairs initiated second or, more infrequently, third clutches between late August and November (Fig. 3, Table 2). MacArthur's (1964) index calculates the length of the breeding season as 4.0 months. The earliest that a clutch was initiated in this study was 23 July (1996), and the latest was 17 November (1997).

The length of the breeding season was determined more by when breeding started than when breeding stopped. Females initiated their first clutch early in 1996 and late in 1995 and 1997 (Table 2; $\chi^2_3 = 61.0$, $p < 0.001$). In contrast, the date that

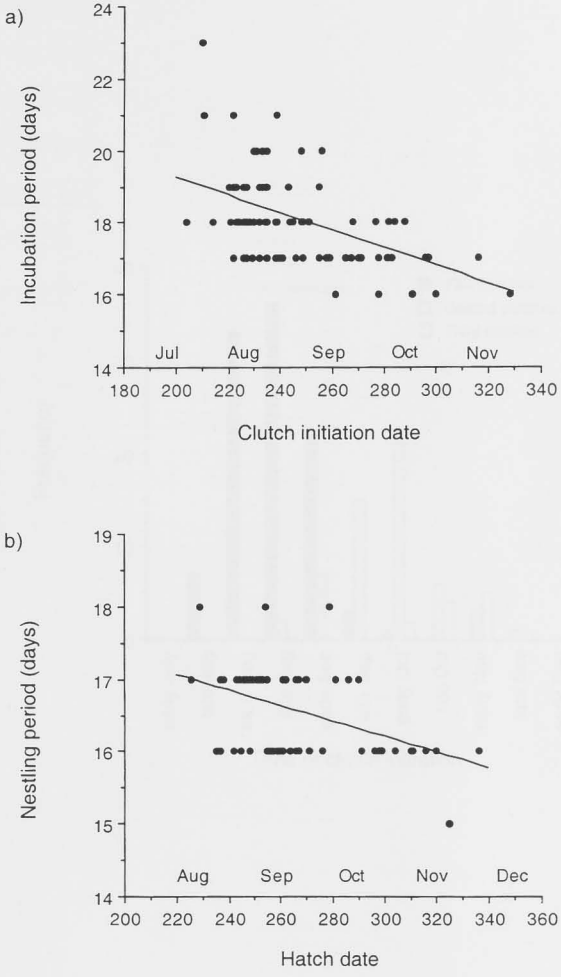


Figure 2. Seasonal changes in a) incubation period and b) nestling period. Lines show predictions from the mixed models. The date used in models is the julian date where January 1 = 1. Data are from all four years of the study; a) n = 92 cases from 58 pairs with 47 females represented, b) n = 63 cases from 43 pairs with 37 females represented.

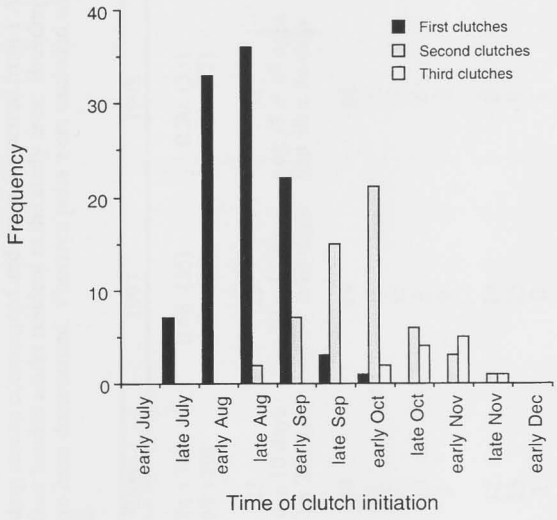


Figure 3. Frequency distribution showing the number of first, second, and third clutches initiated through the breeding season. Data are for the four years combined. Sample sizes are 102, 55, and 12 respectively.

Table 2. Annual patterns of survival, timing of breeding, number of nesting attempts, and reproductive success in the brown thornbill.
The data for each year refer to the year in which the breeding season commenced and cover the period from 1 August in that year until 31 July in the next. Survival data are for all colour banded adults resident in the study area. Breeding data are for all pairs observed sufficiently that all nesting attempts have been documented. Fourteen pairs were excluded when calculating reproductive success in 1998 as their nests were protected.

	1995	1996	1997	1998	Combined
Male survival (N)	0.95 (21)	0.74 (31)	0.66 (35)	0.30 (33)	0.63 (120)
Female survival (N)	0.72 (18)	0.69 (29)	0.71 (28)	0.41 (32)	0.62 (107)
N for timing	15	27	29	31	102
First clutch initiated ± SD	Aug 27 ± 12 days	Aug 10 ± 10 days	Aug 29 ± 11 days	Aug 19 ± 15 days	Aug 21 ± 14 days
Last clutch initiated ± SD	Sep 7 ± 22 days	Sep 22 ± 29 days	Sep 26 ± 28 days	Sep 16 ± 31 days	Sep 19 ± 29 days
N for reproductive success	15	29	29	18	91
Clutches laid- 0	0	2	0	1	3
1	11	7	15	7	40
2	4	18	8	8	38
3	0	2	6	2	10
Broods fledged- 0	6	12	14	8	40
1	9	15	15	9	48
2	0	2	0	1	3
Proportion of pairs that fledge young	0.6	0.59	0.55	0.55	0.57
Fledglings/pair ± SD	1.73 ±1.49	1.72 ± 1.6	1.28 ± 1.31	1.67 ± 1.78	1.57 ± 1.52
Proportion of pairs that produce independent young	0.6	0.55	0.48	0.5	0.53
Ind young/pair ±SD	1.4 ± 1.3	1.03 ± 1.21	0.93 ± 1.1	0.89 ±1.02	1.03 ± 1.15

females initiated their last clutch did not vary significantly over the four years of this study (Table 2; $\chi^2_3 = 4.2$, $p > 0.2$).

Thornbills initiated up to three clutches during a breeding season but rarely fledged more than one successful brood (Table 2). The probability that a pair re-nested was much greater if the first attempt failed (79% of 52 failed attempts) than if it fledged (39% of 38 successful attempts; $\chi^2_1 = 14.9$, $p < 0.001$). For both nests that failed and those that fledged young the date that the previous attempt ended affected the probability that a pair re-nested (Fig. 4; failed attempts- $\chi^2_1 = 24.0$, $p<0.001$; successful attempts- $\chi^2_1 = 9.3$, $p < 0.005$). Since pairs that initiated their first clutch early had more time to re-nest if an early attempt failed the number of clutches initiated by a pair was dependent on when they started to breed ($\chi^2_1 = 10.4$, $p < 0.005$).

The time interval between the date a nest failed or fledged and the time the next clutch was initiated increased with the amount of time invested in the previous nesting attempt (Fig. 5; $\chi^2_3 = 61.2$, $p < 0.001$).

Reproductive success

Seventy-eight per cent of clutches initiated hatched successfully (n = 157 clutches). The major cause of failure was nest predation by birds (n = 27). We suspect this was principally due to pied currawongs *Strepera graculina* which are the most common avian predator in our study area. Additional causes of failure were predation by foxes or feral cats (n = 3), abandonment following the death of a female (n = 3) and nest loss due to high winds (n = 1). Hatching success tended to be lower in September and October than other months (Fig. 6a; $\chi^2_4 = 7.8$, $p < 0.1$).

Young fledged from 48% of clutches that hatched young (n = 123 broods). The major cause of failure was nest predation by birds (n = 39), although some nests were lost to mammalian predators (n = 4) and a few broods were abandoned by males following the death of their mate (n = 5). Predation by snakes or birds was the likely

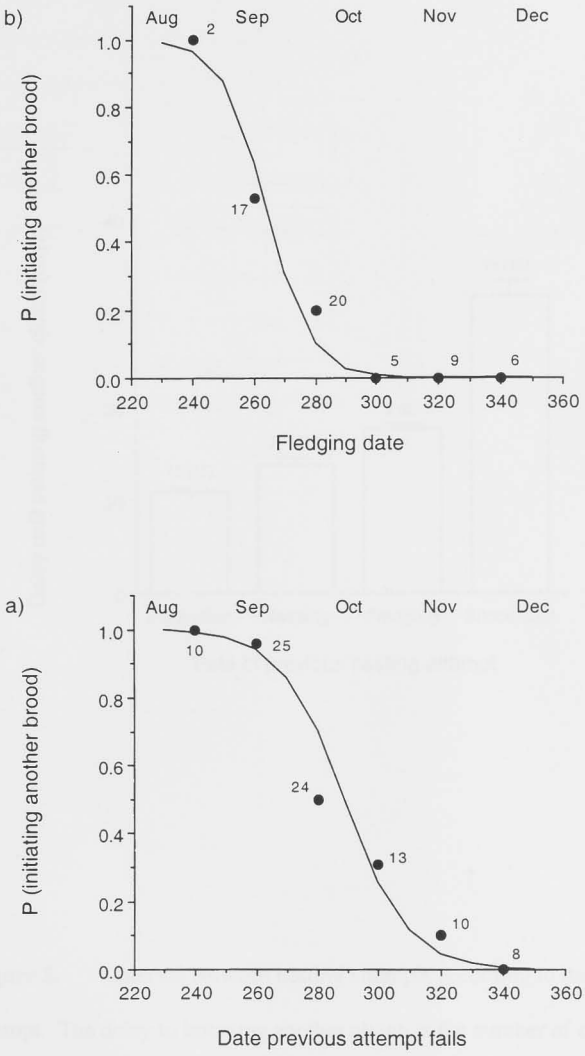


Figure 4. Seasonal changes in the probability of initiating another clutch following a) a failed nesting attempt, and b) a successful nesting attempt. The date used in the model is the julian date where January 1 = 1. The lines are predictions from the mixed models; points show 20-day means with sample sizes.

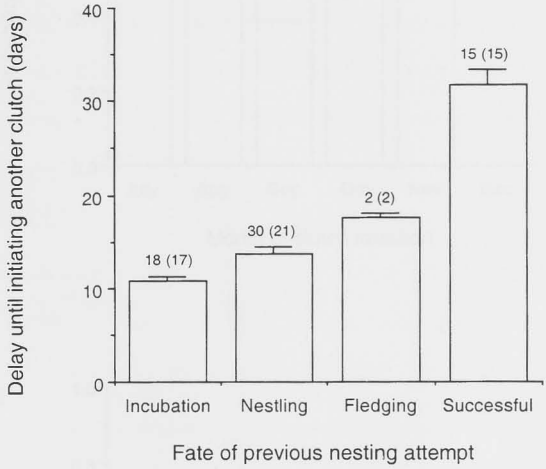
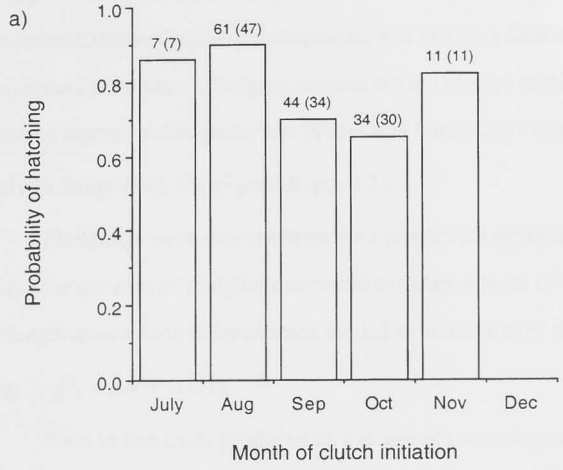


Figure 5. Interval between nesting attempts according to the fate of the previous attempt. The delay to initiating another clutch is the number of days between the failure or fledging of a nesting attempt and the laying of the first egg in the next clutch. Timing of failure is divided into during incubation, during the nestling period, and immediately after fledging; a successful attempt produces at least one independent young. Bars show means + S.E. Numbers are sample sizes while number of pairs represented are in brackets.



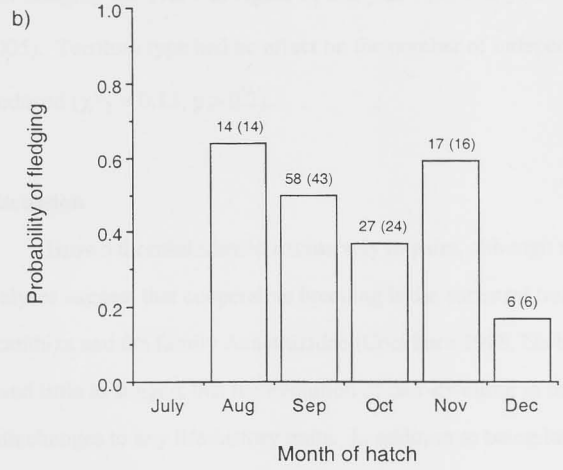


Figure 6. Seasonal pattern to a) hatching success (for all clutches completed) and b) fledging success (for all clutches that hatch). Numbers above bars are number of clutches or broods while number of pairs represented are in brackets.

cause of failure at a further 14 nests where nestlings were removed without any damage to the nest. There were also two known cases of cuckoo parasitism; one by a Fan-tailed Cuckoo *Cuculus pyrrhophanus* and one by a Shining Bronze-cuckoo *Chrysococcyx lucidus*. Fledging success did not change significantly over the breeding season, although the few broods that hatched in December appeared less likely to fledge (Fig. 6b; $\chi^2_4 = 3.6$, $p > 0.2$).

Fledglings were dependent on their parents for approximately six weeks. Sixty-four per cent of fledglings survived to independence (n = 171). The proportion of fledglings reaching independence tended to increase over the breeding season (Fig. 7; $\chi^2_1 = 3.4$, $p < 0.1$).

Pairs in this study produced an average of one independent young per season, but only half the pairs in any year were successful (Table 2). Thornbills were significantly more productive in 1995 than in subsequent years principally because post-fledging survival was higher in that year (Table 2; year effect: $\chi^2_3 = 9.8$, $p < 0.005$). Territory type had no effect on the number of independent young a pair produced ($\chi^2_1 = 0.13$, $p > 0.2$).

Discussion

Brown thornbills breed exclusively in pairs, although recent phylogenetic analyses suggest that cooperative breeding is the ancestral trait both within the genus Acanthiza and the family Acanthizidae (Cockburn 1998, Nicholls et al. 2000). We found little to suggest that the evolution of pair-dwelling in this family is associated with changes to any life-history traits. In addition to being long-lived, brown thornbills possess all of the other life-history traits typical of the cooperatively breeding Acanthizidae (Russell and Rowley 1991, Magrath et al. 2000). They lay small clutches, have long incubation periods, and are able to produce multiple broods over a long breeding season.

Australian passerines have been found to be longer-lived and have higher annual survival rates than equivalently sized passerines in temperate regions of the

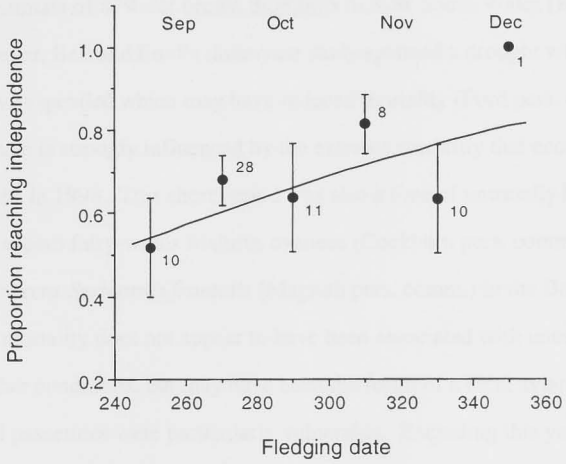


Figure 7. Seasonal change in the proportion of a brood that survives to independence at six weeks. Fledging date used in the model is the julian date where January 1 = 1. The line is the prediction from the mixed model; points show 20-day means with S.E. Numbers adjacent to points are number of broods while number of pairs represented at each point are 10, 26, 11, 8, 10, and 1 respectively.

northern hemisphere (Fry 1980, Rowley and Russell 1991, Yom-Tov et al. 1992). The Acanthizidae can be extremely long-lived and the maximum recorded longevity for a brown thornbill is 17 years (Woinarski 1985, Baker et al. 1999). The estimates for annual survival rates of members within the Acanthizidae based on long-term studies reflect the longevity of this family (Table 3). We estimated the annual survival rates of adult brown thornbills to be 63% which is substantially lower than the estimate of 87% for brown thornbills in New South Wales (Bell and Ford 1986). However, Bell and Ford's three-year study spanned a drought when breeding was partly suspended which may have reduced mortality (Ford pers. comm.). Our estimate is strongly influenced by the extreme mortality that occurred over two months in 1998. This short period was also a time of unusually high mortality for both superb fairy-wrens Malurus cyaneus (Cockburn pers. comm.) and white-browed scrubwrens *Sericornis frontalis* (Magrath pers. comm.) in the Botanic Gardens. The high mortality does not appear to have been associated with unusually cold or wet weather conditions, but may have been the result of a local avian virus to which small passerines were particularly vulnerable. Excluding this year gives an annual survival rate for brown thornbills of 73%. This is likely to be a more accurate estimate as the oldest bird in our study was a minimum of 11 years old when last re-sighted, and three are currently at least 7 years old.

Social organisation

The majority of well studied *Acanthiza* species have been reported to breed cooperatively, although the proportion of birds that breed in groups rather than pairs varies considerably between species and also between populations within species. For example, although striated thornbills *A. lineata* in northern New South Wales frequently breed in groups (43% of breeding units, n = 14, Bell and Ford 1986), yellow-rumped thornbills *A. chrysorrhoa* in the Australian Capital Territory rarely do so (7% of breeding units, n = 46, Ebert pers. comm.). In contrast we found that brown thornbills breed exclusively in pairs. No pairs were helped by additional birds at any stage of the breeding cycle over the four years of this study (n = 105 pair-

years). Brown thornbills are also reported to breed strictly in pairs in New South Wales, South Australia, and Tasmania, so are likely to be pair-breeding throughout their range (Wheeler 1960, Thomas 1965, Bell and Ford 1986).

The pair defended a permanent territory which ranged in size from 0.4 to 3.1 hectares throughout the year. Territory size may reflect food availability in different habitats as territories in artificially watered plantations were smaller than those in natural woodland. Additional support for this hypothesis is provided by Bell and Ford (1986) who found that although territory sizes varied they contained approximately the same amount of understorey, the preferred foraging niche of brown thornbills.

Breeding Biology

Brown thornbills typically laid a clutch of three eggs. Small, relatively invariate, clutches are characteristic of the Acanthizidae and seem likely to be ancestral traits within the Corvida (Yom-Tov 1987, Woinarski 1989, Ricklefs 1993, Magrath et al. 2000). Small clutch sizes may have evolved in response to an aseasonal environment where there is little or no peak in food availability to support reproduction (Ashmole 1963, Woinarski 1985). The relatively minor winter decline in arthropod abundance in the foliage of forests in south-eastern Australia support this hypothesis (Woinarski and Cullen 1984, Woinarski 1985). The lack of seasonal variation in the clutch size of brown thornbills is also consistent with a lack of seasonality in conditions for breeding (Crick et al. 1993). However, at this point we have no direct evidence that food supply during the nestling period constrains clutch size.

The two-day laying interval which appears to be a feature of the Acanthizidae (Magrath et al. 2000) has also been attributed to an inadequate food supply (Thomas 1974). However, the fixed two-day laying interval in brown thornbills and other members of the Acanthizidae suggests that food is unlikely to be a proximate factor in this family. The two-day laying interval may allow females to lay relatively large eggs and thus improve the growth or survival of young, without impairing their

foraging ability or making them more vulnerable to predation (Williams 1994, Magrath et al. 2000,). Female thornbills do produce large eggs, a clutch weighs approximately 61% of their body weight, providing some support for this hypothesis.

Long incubation periods are characteristic of the Acanthizidae (Ricklefs 1993). Ricklefs has suggested that long incubation periods may assist in the maturation and subsequent efficiency of the immune system, and found that long incubation periods are associated with high annual adult survival and low prevalence of blood parasites (Ricklefs 1992, 1993). Brown thornbills have a mean incubation period of 18.0 days which is much longer than the 12.4 days predicted for a passerine with a mass of 6.4 g or the 12.7 days for a passerine laying an egg of 1.3 g (Rahn et al. 1995). Brown thornbills also have high annual adult survival rates and individuals may live for up to 17 years which is consistent with Ricklefs' hypothesis (Bell and Ford 1986, Wilson 1995, Baker et al. 1999, this study).

We found that both the incubation and nestling period declined over the breeding season. The marked seasonal decline in the incubation period probably reflects the change in temperature between August (mean daily max = 13°C) and November (mean daily max = 23°C) when clutches are being incubated. Females are presumably able to keep eggs at optimal temperatures for a greater proportion of the time when it is warmer. It is less clear why the nestling period also declined through the season. We found no evidence to suggest that nestlings grow faster when ambient temperatures are higher; age specific nestling mass does not increase through the season (unpublished data). Perhaps, the time at which nestlings fledged changed because of a shift in the relative predation rates in and out of the nest; nest predation rates increased slightly while fledgling loss decreased over the breeding season.

Species within the Australian endemic family, the Acanthizidae, are thought to have long breeding seasons compared to similar insectivorous birds in the northern hemisphere which typically breed for 2-3 months (Woinarski 1985). We found that brown thornbills do have a comparatively long breeding season (4.0 months), clutches were initiated from mid-winter until late spring.

Brown thornbills were thought not re-nest if their first clutch was successful (Bell and Ford 1986). However, we found that pairs not only initiated a second clutch if their first failed, but also frequently (ca. 40%) re-nested if their first attempt was successful. Multi-brooding was more common in years when breeding started early as pairs that did not fledge their first brood early in the season were unlikely to re-nest. Brown thornbills may not have been reported to fledge two broods in northern New South Wales (Bell and Ford 1986) because high predation rates meant females were unable to fledge their first brood sufficiently early in the season. Females are less likely to re-nest after a successful breeding attempt than after a failed attempt presumably because of the long period of post-fledging care provided and the costs associated with caring for fledglings. Females also take longer to re-nest after attempts that fail during the nestling period or immediately after fledging than after attempts that fail during incubation. Furthermore, females provisioning young weigh less than at other times of the year (unpublished data). These data all suggest that females face energetic constraints that limit when and if they are able to initiate a new clutch.

Seasonal patterns to reproductive success

Predation rates on the domed nests built by female brown thornbills were low both prior to hatching (1.2% per day), and during the nestling period (4.0% per day). This is much lower than those reported for similar northern hemisphere species (mean predation rates on eggs and nestlings 9.3% and 8.4% respectively; Clark and Wilson 1981). Predation rates were relatively constant throughout the breeding season, although there was some suggestion that predation rates on both eggs and nestlings increased in September and October. This coincides with the period when pied currawongs are foraging on a diversity of avian prey; they switch to a diet composed largely of fairy-wren nestlings later in the breeding season (Prawiradilaga 1996).

Post-fledging survival to independence at six weeks tended to increase over the breeding season. We are not certain why this should be the case. The majority of

the mortality occurred in the first few days after fledging which suggests that predation may play a role. Perhaps, pied currawongs expend less effort hunting fledgling thornbills later in the season when their principal prey, nestling fairy-wrens, are at their most abundant. Alternatively, harsher climatic conditions in September may simply make it harder for fledglings to survive the first few days out of the nest early in the season.

Demography of pair-dwelling and cooperatively breeding species in the Acanthizidae

Cooperative breeding in birds is rare and has generally been assumed to be a derived condition which has evolved from pair-breeding (Lack 1968). Recent phylogenetic analyses, however, suggest that evolution can progress in both directions (Peterson and Burt 1992, Cockburn 1998). Within the Acanthizidae it is now apparent that pair-breeding has evolved independently at least four times, twice within the genus *Acanthiza*, once within the genus *Gerygone* and once within the genus *Sericornis* (Nicholls et al. 2000).

Examination of the demography of species within the Acanthizidae provides little evidence to suggest that pair-breeding within the Acanthizidae is linked to an increase in adult mortality, a short breeding season with reduced productivity, or high levels of predation post-fledging (Table 3). This conclusion is consistent with those of a comparative analysis that found no difference between the life-history traits of cooperatively and non-cooperatively breeding Corvida within Australia (Poiani and Jermiin 1994).

Arnold and Owens (1998, 1999) have argued that while variation in life history is important in determining which avian lineages are predisposed to cooperative breeding, ecological factors will determine which species in these predisposed lineages actually breed cooperatively. However, there appear to be no broad ecological factors that correlate with the occurrence of pair or cooperative breeding within the Acanthizidae. Ford et al. (1988) and Cockburn (1996) have suggested that species living in dense habitat are more likely to breed in pairs.

Table 3. Comparison of the population demography of pair-dwelling and cooperatively-breeding species in the Acanthizidae. The data presented is restricted to long-term studies conducted on colour banded populations of birds.

		Social system	Survival			Breeding season* (months)	Productivity (fledglings/pair or group)	Post-fledging survival to independence %	Reference
			male	female	adult				
Brown Thornbill	(i)	Pair-dwelling	0.63	0.62	0.63	4.0	1.57	64	this study
Acanthiza pusilla	(ii)	Pair-dwelling	-	-	0.87	3.8	-	-	Bell and Ford 1986
Grey Gerygone *Gerygone igata*		Pair-dwelling	-	-	0.82	3.6	4.04	54	Gill 1982
Buff-rumped Thornbill	(i)	Cooperative	-	-	0.58	3.3	1.11	83	Bell and Ford 1986
Acanthiza reguloides	(ii)	Cooperative	-	-	-	4.6	1.70	-	Ebert pers. comm.
Yellow-rumped Thornbill	(i)	Cooperative	-	-	-	5.5	3.60	-	Ford 1963
Acanthiza chrysorrhoa	(ii)	Cooperative	0.68	0.59	0.64	3.8	1.45	-	Ebert pers.comm.
White-browed Scrubwren *Sericornis frontalis*		Cooperative	0.85	0.79	0.82	5.4	2.80	63	Magrath and Yezerinac 1997
Speckled Warbler *Chthonicola sagittata*		Cooperative	0.69	0.61	0.66	5.0	0.84	64	Gardner pers. comm.

* calculated from the original data using MacArthur's index for the length of the breeding season (1964)

Although brown thornbills do breed in habitat with dense understorey, the two species of *Acanthiza* that breed exclusively in rainforest appear to both breed cooperatively (Nicholls et al. 2000). Similarly, although the one pair breeding member of *Sericornis* (*S. citreogularis*) typically breeds in dense forest gullies the cooperatively breeding congeners also breed in dense habitat (Keast 1978, Nicholls et al. 2000).

The absence of any life-history or broad ecological correlates with mating system in the Acanthizidae makes it unclear why pair-breeding has evolved several times in this family. Cockburn (1996) has suggested that although there may be general advantages to juveniles of prolonged philopatry and extended parental care in the Corvida, the costs of juvenile retention to adults may sometimes result in a conflict of interest between parents and young. The active eviction of young from their natal territory in the pair-breeding white-throated treecreeper (*Cormobates leucophaea*), which does not occur in two cooperatively breeding species (*Climacteris picumnus* and *C. erythrops*), provides evidence of such conflict (Noske 1991). Retention of juveniles may be costly to parents if they depress limiting resources on their natal territory (Koenig *et al.* 1992). An alternative cost to parents of young remaining on their natal territory is conflict over reproduction (Cockburn 1996). Further study focussed on conflict between parents and young may therefore shed light on the evolution of pair-breeding in the *Acanthiza*.

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Chapter 3

The influence of age on reproductive performance in the brown thornbill

Journal of Avian Biology (in press)

Abstract

I examined age effects on reproduction in the brown thornbill *Acanthiza pusilla* in Canberra, Australia. I found that the reproductive performance of both males and females improved with age, although only age-related improvement in male performance had a significant effect on annual reproductive success. Reproductive success improved with male age as a result of improved performance during two stages of the breeding cycle: first-year males were less likely to fledge young than those aged two or more, while both first and second-year males were less successful at raising fledglings to independence than males of three or more. Male performance appears to improve over three years as they gain experience at provisioning nestlings and caring for fledglings without attracting predators, rather than as a direct result of improved foraging skills. In contrast, reproductive success only improved slightly with female age, although females of two or more years initiated their first clutch earlier in the season than one-year-old females, and tended to be more likely to re-nest if a breeding attempt failed. The poor performance of young females appears unlikely to be related to their foraging ability but may be associated with costs imposed by dispersing to a breeding vacancy earlier in the year. Although the reproductive performance of brown thornbills improves considerably with age I found no evidence that performance improved as a result of repeated breeding attempts with the same partner.

Introduction

In the majority of birds reproductive success improves with age during the first few years of reproductive life (Clutton-Brock 1988, Newton 1989, Saether 1990). Female reproductive success may be enhanced as a result of improvement in a number of life-history traits including the timing of breeding, egg size, clutch size, and offspring rearing ability (eg. Coulson 1966, Robertson et al. 1994, De Steven 1978, Daunt et al. 1999). The influence of male age on the reproductive success of monogamous birds has been less well documented. Nevertheless, studies on a wide range of species have found that male reproductive success also improves with age even after controlling for the age of their mate (eg. passerines: McCleery and Perrins 1988; raptors: Newton 1988; sea-birds: Pyle et al. 1991). Despite the pervasiveness of age-related improvement in the reproductive performance of birds, the reasons behind this pattern are still poorly understood.

Three hypotheses have been generated to explain patterns of age-specific reproductive performance (Part and Forslund 1995). First, the mean reproductive success of a cohort may improve with age simply because of the higher mortality of phenotypically inferior individuals (Curio 1983). This explanation predicts that individuals that do not perform well in reproduction also have a lower probability of survival. Second, the greater reproductive success of older birds may be attributed to age-related improvement in a skill that positively affects breeding performance (Curio 1983, Nol and Smith 1987). Skills that can improve with age include foraging ability, nest-site selection, coordination of parental duties, predator detection and avoidance, and the ability to raise chicks (Desrochers 1992, Bradley et al. 1990, Ainley and Schlatter 1972, Martin 1995). Many of these skills may improve as a result of breeding experience, obtained both as an individual and jointly with a partner, rather than as a direct consequence of age. Finally, life-history theory suggests that reproductive success may increase because individuals increase their reproductive effort, or the fraction of available resources allocated to reproduction, with age. Individuals are predicted to increase their reproductive effort if their expectation of future survival and reproduction decreases with age owing to

senescence (Charlesworth 1980, Curio 1983, Williams 1966). Alternatively, individuals are expected to limit the amount of resources they allocate to reproduction when young if age-related improvement in competence means the return for a given level of effort is greater at older ages (Charlesworth 1980, Pianka and Parker 1975).

In this paper I report on the effects of age on the reproductive performance of female and male brown thornbills, a long-lived passerine endemic to Australia. This is the first study of age effects on reproduction for any member of the Acanthizidae. I determine at what stage of the breeding cycle the effects of female and male age on performance are most marked and examine how parental ages interact to influence overall reproductive success. I also investigate whether pair-bond duration has any effect on breeding performance after controlling for the ages of the pair. Finally, I discuss why reproductive performance improves with age in the brown thornbill.

Methods

Study area and general methods

I conducted this study on a colour-banded population of brown thornbills in and adjacent to the Australian National Botanic Garden in Canberra, Australia, from July 1995 to September 1999. The vegetation in the Botanic Gardens consists of plantations of Australian native trees and shrubs and natural woodland, which is contiguous with a large area of dry sclerophyll forest in Black Mountain Nature Reserve. Brown thornbills are small (ca. 7g), yet long-lived (up to 17 years), insectivores that are common throughout the eucalypt forests and woodlands of south-eastern Australia (Baker et al. 1999). Pairs defend small territories (ca. 2 ha) year round (Bell and Ford 1986). Individual females lay up to three clutches, which almost always contain three eggs, and fledge up to two broods during the four-month breeding season that starts in late-July. Females build the nests and incubate without assistance, but males contribute to nest defence and the provisioning of nestlings and fledglings (Chapter 2).

I monitored the study population throughout the year. During the non-breeding season (January to June) I visited the study area at least once a month to census pairs, document survival, and identify when new birds entered the population. Survival of colour-banded adults was measured from the start of one breeding season (August 1), until the beginning of the next. I assumed birds had died if, after being a member of a breeding pair, they disappeared and were not seen again. During the breeding season each pair was monitored at least three times a week to ensure that I documented all nesting attempts even if they failed during incubation. I recorded laying dates by direct observation (73% of nests were found before laying was completed) or by estimation using the hatching date and regression of incubation period on clutch initiation date (Chapter 2). Hatching and fledging dates were determined by daily visits to the nest towards the end of the incubation and nestling period, respectively. Nests at which no young fledged were assumed to have failed on the day after the nest was last known to have been active. The proportion of a brood surviving to independence, six weeks after fledging, was determined by weekly censuses conducted between two and eight weeks post-fledging. Nestlings were weighed when 6-10 days old, and in 1997 and 1998, also when aged 11-12 days. The condition of all nestlings was estimated using residuals from sex-specific logistic growth curves, and the brood mean was used as a measure of the condition of the brood.

Aging and sexing individuals

The proportion of birds that could be categorised as being either one, two, or at least three years old, increased from 27% in 1995 to 81% in 1998 (Table 1). Forty-two birds that entered the breeding population were of known age. Nineteen of these were banded as nestlings. I classified a further four birds as juveniles on the basis of eye colour when first caught. Juvenile brown thornbills have brown eyes whereas those of an adult are red (Rogers et al. 1986). I also assumed that 19 birds which traversed more than one territory to fill a vacancy were juvenile birds, even if they had red eyes when captured for the first time. This is a reasonable assumption

Table 1. Age-structure of males and females and pair status of Brown Thornbills studied in the Australian National Botanic Gardens, 1995-1998.

	1995	1996	1997	1998
Male age (years)				
One	0	3	6	4
Two	1	0	4	8
Three plus	4	8	13	15
Unknown	10	18	6	5
Female age (years)				
One	0	4	9	7
Two	0	0	3	7
Three plus	3	4	9	11
Unknown	12	21	8	7
Pair status				
New pair	0	9	19	17
Established pair	0	12	10	13
Unknown	15	8	0	2
N	15	29	29	32

because juveniles attain adult characteristics after only 3-4 months, and adult brown thornbills are relatively sedentary (Wilson 1995). Adults in this study never moved more than one territory following divorce or the death of their mate.

I sexed all birds using a simple PCR-based molecular technique using DNA extracted from a blood sample taken when they were first banded (see Griffiths et al. 1998 for details of the method). The results obtained using this technique were always consistent with those obtained using behavioural data (Chapter 2).

Statistical analysis

I collected data from pairs that made multiple nesting attempts in one season and were sometimes present for more than one year of the study, resulting in data that were not independent. Mixed models are necessary to analyse such data appropriately as they do not require equal sample sizes and incorporate random as well as fixed effects (Bennington and Thayne 1994). Random effects are used to account for the dependence of data collected from the same pair. I used "pair identity" as a random factor in all mixed models. A new pair was considered to have formed when either member was replaced following a death or divorce.

I examined the effect of age and pair-bond duration had on reproduction in brown thornbills by fitting separate mixed models to ten response variables. Eight response variables were associated with individual breeding attempts: the length of the incubation and nestling period, the likelihood that a pair would re-nest following a failed breeding attempt, the time interval between failure and re-nesting, hatching success (for all clutches that were initiated), the condition of the brood, fledging success (for all clutches that hatched), and the proportion of a brood surviving to independence (for all broods that fledged). Two response variables were associated with the timing of breeding and reproductive success over the entire breeding season: the date a pair initiated their first clutch of the year, and the number of independent young they produced during the season. I used three principal explanatory variables in the models: female age (1, 2, 3+), male age (1, 2, 3+), and pair-bond duration (new or established pair). I also included year, and either month or Julian date in models

when these terms were needed to control for any variation in breeding performance between years and across the breeding season. Month was used in preference to Julian date when the seasonal effect was non-linear. Chapter 2 provides details of annual and seasonal variation in the breeding performance of brown thornbills in this population.

Mixed models were fitted using Genstat v. 5.3.2 (Genstat 1993). Continuous response variables were analysed using the restricted maximum likelihood (REML) procedure while binary response variables were analysed using the generalised linear mixed model (GLMM) procedure. I initially fitted models containing male age, female age, and any term needed to control for annual and seasonal variation in reproduction, plus all two-way interactions between these terms. A final model was selected after sequentially dropping all non-significant ($p > 0.05$) interaction terms from the models. Main effects were not dropped from the models. The effects of age on reproduction were therefore evaluated after controlling for both, annual and seasonal variation in reproduction, and the age of their partner. I subsequently examined whether pair-bond duration had any additional effect on reproduction after controlling for any significant age and annual/seasonal effects. Sample sizes varied slightly between analyses because nests were found, and failed, at different times during the breeding cycle. I also excluded any pairs from analyses of hatching, fledging, and annual reproductive success whose nests were protected as part of an experiment in 1998.

Survival data were analysed using logistic regression models as implemented in JMP v. 3 (SAS Institute). In all models residual plots and normal probability plots were used to examine for unequal variances and deviations from normality among residuals. Model predictions are presented as means ± the standard error, or means with the standard error of differences (Genstat 1993).

Results

Pair-bond formation

Brown thornbills breeding together for the first time did not appear to pair assortatively with respect to age. First-year males and females were as likely to pair with an older partner as a partner of their own age (Table 2). Consequently, I was able to separate the effects of male age and female age on reproductive performance in brown thornbills.

Timing of breeding

Female thornbills always attempted to breed when one year old (n = 22) and the majority of males (80%, n = 20) also bred for the first time when one year old. The four males that did not breed in their first year established territories when one year old but did not acquire mates until they were two.

One-year-old females initiated their first clutch about two weeks later than females of two or three-plus years (Fig. 1, Table 3). The date that females initiated their first clutch also varied between years (year effect: $\chi^2_3 = 17.5$, $p = 0.0006$). Male age and pair-bond duration had no effect on when pairs started to breed (Table 3).

Length of the incubation and nestling period

There was a significant seasonal decline in the length of both the incubation period and the nestling period (incubation period: date effect, $\chi^2_1 = 26.8$, $p < 0.0001$; nestling period: date effect, $\chi^2_1 = 14.3$, $p = 0.0002$). Female age, male age and pair-bond duration had no effect on the length of either the incubation period or the nestling period (Table 3).

Probability of re-nesting and the interval between nesting attempts

The probability of a pair re-nesting following a failed breeding attempt declined over the breeding season (date effect, $\chi^2_1 = 14.3$, $p = 0.0002$). One-year-old females tended to be less likely than females of two or three-plus to re-nest (GLMM

Table 2. Age-composition of newly formed Brown Thornbill pairs.

	Female age (years)		
Male age (years)	One	Two	Three-plus
One	6	1	4
Two	3	2	1
Three-plus	9	3	2

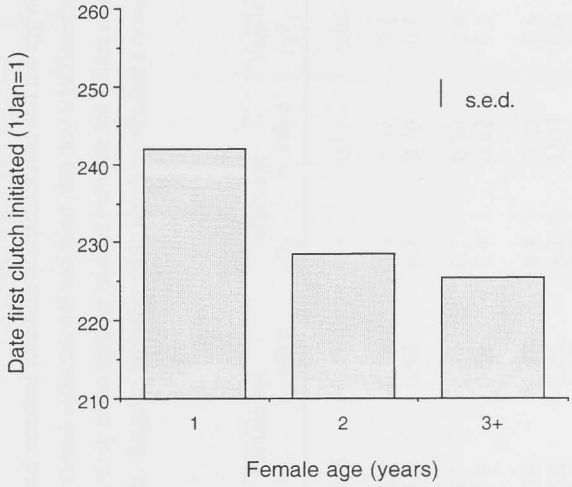

Figure 1. Relationship between female age and the date a pair initiate their first clutch of the year after controlling for both the age of their mate and variation between years. Bars show the predicted means from the REML model and the line shows the average standard error of differences (s.e.d.). The model draws on data from 49 pair-years and 39 pairs

Table 3. Model summaries for effects of age and pair-bond duration on reproduction in male and female Brown Thornbills.

The age effects presented control for any significant annual and seasonal variation in reproduction and the age of the partner. Pair-bond duration effects are examined after controlling for annual and seasonal variation plus any significant age effects. Dates in all models take the form 1 Jan = 1. Delay until re-nesting is the number of days between the failure of a nesting attempt and the laying of the first egg in the subsequent clutch. Stage of breeding cycle refers to whether a nesting attempt failed during incubation or the nestling period.

Response variable	Annual or seasonal effects	Female age		Male age		Pair-bond duration	
		χ^2_2	p- value	χ^2_2	p- value	χ^2_1	p- value
Date first clutch initiated	year	20.8	< 0.0001	1.2	0.55	0.02	0.89
Incubation period	date clutch initiated	2.9	0.23	0.9	0.64	0.1	0.75
Nestling period	hatch date	1.4	0.50	0.7	0.70	0.1	0.75
Relay if attempt failed	date failed	5.7	0.06	0.7	0.70	1.6	0.21
Ln (delay until re-nesting)	stage of breeding cycle	0.9	0.64	0.4	0.82	0.1	0.75
Hatching success	month clutch initiated	0.8	0.67	0.3	0.86	2.5	0.11
Fledging success	-	3.0	0.22	5.3	0.07*	0.0	1.0
Proportion of brood surviving to independence	date fledged	2.1	0.35	8.7	0.01	0.7	0.40
Condition of brood	year*hatch date	1.8	0.41	1.4	0.49	0.7	0.40
Number of independent young produced		2.1	0.35	14.6	< 0.001	0.4	0.82

* see text for further statistical evaluation of this result.

model predictions after controlling for male age: 1-year-old = 0.30 ± 0.14, 2-year-old = 0.83 ± 0.20, 3+ year-old = 0.75 ± 0.11, Table 3). Since older females also initiated their first clutch of the year earlier in the season the number of clutches initiated per season increased significantly with female age (REML model predictions controlling for male age: 1-year-old = 1.14 clutches, 2-year-old = 1.64, 3+ year-old = 2.02, s.e.d. = 0.30; $\chi^2_2 = 12.8$, $p = 0.002$). Male age and pair-bond duration had no affect on the probability that a pair re-nested following a failed breeding attempt (Table 3).

The mean delay until females initiated a new clutch was not affected by female age, male age, or pair-bond duration (Table 3). However, the delay was shorter following nesting attempts that failed during incubation than nesting attempts that failed during the nestling period (stage of breeding cycle effect: $\chi^2_1 = 4.3$, $p = 0.04$).

Hatching success

Clutches initiated in September and October had a significantly lower probability of hatching than those initiated in other months (month effect: $\chi^2_4 = 9.8$, $p = 0.04$). However, female age, male age, and pair-bond duration all had no effect on the probability that a clutch hatched (Table 3).

Fledging success

One-year-old males tended to be less likely to fledge young than males aged two or three-plus (Fig. 2a, Table 3). The model is, however, likely to underestimate the statistical importance of age because the alternative hypothesis does not explicitly consider the expectation that there is an ordered increase in the mean with age (Gaines and Rice 1990, Rice and Gaines 1994). To address this concern, and since the difference in fledging success appeared to be primarily between first-year and older males, I re-ran the model examining fledging success with male age categorised as one or two-plus. Broods provisioned by one-year-old males were less

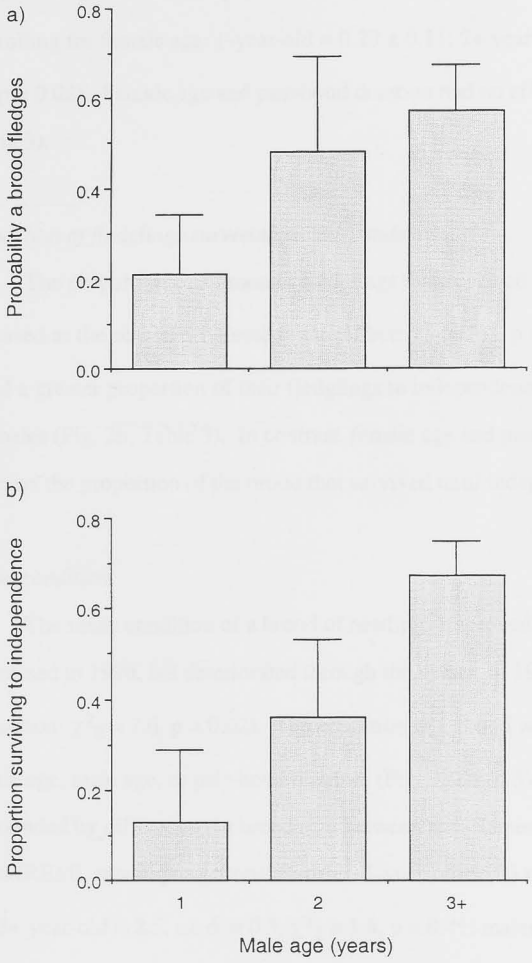

Figure 2. Relationship between male age and a) the probability of fledging a brood (for all clutches that hatch), and b) the proportion of fledged young that are raised to independence, controlling for the age of their mate. Bars show the predicted means ± s.e. from the GLMM models. The two models draw on data from: (a) 55 brood produced by 35 pairs and (b) 28 broods produced by 24 pairs.

likely to fledge than broods provisioned by older males (GLMM model predictions controlling for female age: 1-year-old = 0.20 ± 0.11; 2+ year-old = 0.52 ± 0.08; χ^2_1 = 5.6, p = 0.02). Female age and pair-bond duration had no effect on fledging success (Table 3).

Proportion of fledglings surviving to independence

The proportion of a brood of fledglings that survived to independence increased as the season progressed (date effect: χ^2_1 = 5.1, p = 0.02). Old males also raised a greater proportion of their fledglings to independence than one or two-year-old males (Fig. 2b; Table 3). In contrast, female age and pair-bond duration had no effect on the proportion of the brood that survived until independence (Table 3).

Brood condition

The mean condition of a brood of nestlings improved as the season progressed in 1996, but deteriorated through the season in 1997 and 1998 (year-date interaction: χ^2_2 = 7.6, p = 0.02). The condition of a brood was not affected by female age, male age, or pair-bond duration (Fig. 3, Table 3). This result was not confounded by differences in brood size between age-classes or pairs of differing status (REML model predictions: females, 1-year-old = 2.3 nestlings, 2-year-old = 2.1, 3+ year-old = 2.5, s.e.d. = 0.3, χ^2_2 = 1.8, p = 0.41; males, 1-year-old = 2.2 nestlings, 2-year-old = 2.2, 3+ year-old = 2.5, s.e.d. = 0.4, χ^2_2 = 1.4, p = 0.49; status, new pair = 2.4 nestlings, established pair = 2.6, s.e.d. = 0.2, χ^2_1 = 0.7, p = 0.40).

Annual reproductive success

The number of independent young produced by a pair increased with male age (Fig. 4, Table 3). Pairs with one-year-old males produced very few independent young, whereas pairs with males of two or three-plus years were progressively more successful. The reproductive success of a pair did not improve significantly with

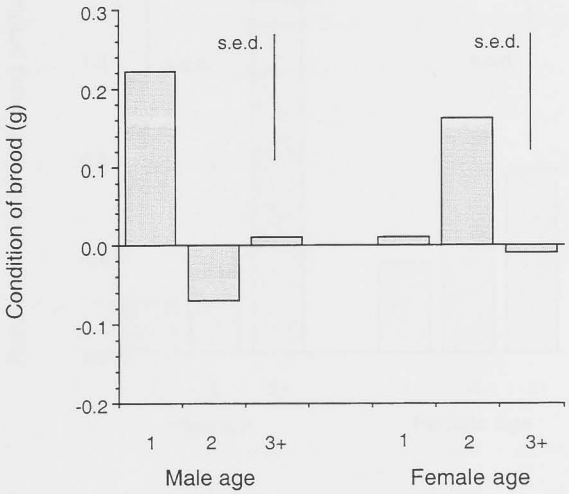

Figure 3. Relationship between male and female age and the condition of a brood after controlling for the age of their mate. Nestling condition is determined using the residuals from sex-specific logistic growth curves and the brood mean is used to estimate the condition of a brood. Bars show the predicted means from the REML model and the lines the average standard error of differences (s.e.d.). The model draws on data from 51 brood produced by 34 pairs.

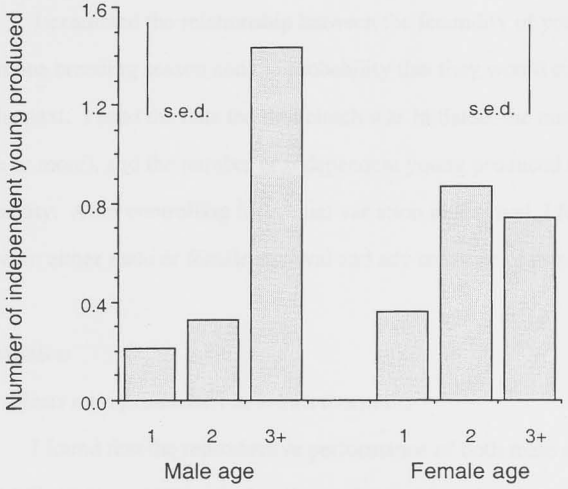

Figure 4. Relationship between male and female age and reproductive success after controlling for the age of their mate. Bars show the predicted means from the REML model and the lines the average standard error of differences (s.e.d.). This model draws on data from 46 pair-years and 38 pairs.

female age, although the pattern was for one-year-old females to be less successful than older females (Fig. 4, Table 3). Pair-bond duration had no affect on the reproductive success of a pair after controlling for the age of the male (Table 3).

Fecundity and survival

I examined the relationship between the fecundity of young birds (aged 1 and 2) in one breeding season and the probability that they would survive until the start of the next. I used the date the first clutch was initiated, the number of clutches laid (one or more), and the number of independent young produced as measures of fecundity. After controlling for annual variation in survival, I found no relationship between either male or female survival and any measure of fecundity (Table 4).

Discussion

Age effects on reproduction in brown thornbills

I found that the reproductive performance of both male and female brown thornbills improved with age, but that males and females showed age related improvement at different stages of the breeding cycle. Male breeding performance improved with age at two stages of the breeding cycle: males of two or more years were more likely to raise nestlings to fledging than yearling males, and males of three or more raised a significantly higher proportion of their fledglings to independence than males of either one or two years. As a result, male reproductive success improved dramatically over the first three years of life. In contrast, female age influenced the timing of breeding and the number of breeding attempts initiated. Females of two years or more initiated their first clutch approximately two weeks earlier than females in their first year and tended to be more likely to re-nest if a breeding attempt failed. Females of two or more years therefore had slightly higher reproductive success than females of one year, although this difference was not statistically significant. Few other studies have examined the independent effects of male and female age on reproduction in monogamous passerines. Our results are

Table 4. Summary statistics from the logistic regression models examining fecundity effects on survival in male and female brown thornbills after controlling for the effects of year.

	n	χ^2_1	p-value
Males			
Initiation date	26	0.14	0.70
Number of clutches	22	2.30	0.13
Number of independent young	22	0.18	0.67
Females			
Initiation date	26	1.23	0.27
Number of clutches	25	1.63	0.20
Number of independent young	25	0.30	0.58

similar to those of McCleery and Perrins (1988, 1989) who found that while female age had an effect on clutch size and the timing of breeding in great tits *Parus major*, only male age had a significant effect on the number of young recruited. In contrast, most other studies have found that only female age has a significant effect on reproductive success (eg. European blackbirds *Turdus merula*, Desrochers and Magrath 1996; splendid fairy-wrens *Malurus splendens*, Russell and Rowley 1996).

Why does reproductive performance improve with age?

Positive relationships between fecundity or reproductive success and age may arise as a result of the selective mortality of inferior phenotypes or because superior individuals defer breeding until a greater age (Curio 1983). Current evidence from empirical studies suggest, however, that differential survival and delayed reproduction play little or no part in the observed age differences in reproductive performance of birds (Forslund and Part 1995, for an exception see Nol and Smith 1987). I found little evidence to refute this conclusion. There was no relationship between either male or female survival and any measure of fecundity or reproductive success. There was also little variation in the age at first breeding: all female thornbills and the majority of males breed for the first time as yearlings. It appears likely, therefore, that the observed pattern of age-related improvement in reproductive performance by thornbills represents actual improvement in the breeding performance of individuals with age.

Life history theory suggests that individuals should increase their reproductive effort with age as a response to a reduction in their residual reproductive value (Williams 1966, Gadgil and Bossert 1970, Charlesworth 1980, Pianka and Parker 1975). However, brown thornbills have a low annual mortality rate that remains constant throughout life (Bell and Ford 1985, Wilson 1995) so their residual reproductive value should not decline due to mortality effects during the early stages of their reproductive life (Forslund and Larsson 92). It is unlikely, therefore, that brown thornbills increase their reproductive effort early in life in response to decreasing residual reproductive value. Increased reproductive effort

alone is therefore insufficient to account for the observed improvement in reproductive performance with age.

The results of this study, although not based on longitudinal data, suggest that the major factor responsible for the age-related improvement in reproductive performance in the brown thornbill is improved skill with age. The improvement in skill will have a direct effect on reproductive success, but may also result in individuals increasing their reproductive effort, as the returns for a given level of investment will be greater at older ages. Determining the relative importance of changes in reproductive effort to overall reproductive success ideally requires measurement of age-specific reproductive effort and an understanding of the mechanism underlying the age-related improvement in performance (Forslund and Part 1995). I did not attempt to measure reproductive effort but the absence of any age effects on the condition of nestlings does not suggest restraint on the part of young thornbills.

Age and female performance

Studies on a diversity of avian taxa have found that female age has a pronounced effect on the timing of breeding (see Saether 1990 for a review). Lack (1968) and Perrins (1970) first suggested that young individuals may delay reproduction because they are less efficient and skilful than older individuals at exploiting food. Two recent studies have confirmed that the foraging efficiency of breeding birds improves with age (Desrochers 1992a, Jansen 1990). Desrochers (1992b) verified that poor foraging ability delays breeding in female European blackbirds by experimentally increasing food availability for young blackbirds, which removed any effect of age on reproductive performance.

Female thornbills in their first year initiate their first clutch much later than older females, and tend to be less likely to re-nest if a breeding attempt fails, suggesting that they may face an ecological constraint on reproduction that is similar to blackbirds. I did not measure the foraging ability of female thornbills immediately prior to reproduction in the Austral winter. However, I have little evidence to

suggest that foraging ability during the breeding season improves with age since female age had no effect on the mean condition of nestlings in a brood and brood size did not vary among age-classes. Alternatively, first-year-females may be in worse condition than older females at the end of winter as a result of dispersing from their natal territory earlier in the year. They may therefore take longer to accumulate the body reserves required to initiate a clutch. Food supplement experiments, which in multi-brooded species generally advance laying date, provide some support for this hypothesis (Boutin 1990, Daan et al. 1988).

Age and male performance

Previous studies have suggested that incubation of eggs, chick-rearing ability, the detection and deterrence of nest predators, and post-fledging care may all improve as a result of prior experience (eg. Daunt et al. 1999, Lessells and Krebs 1989, Pyle et al. 1991, Reid 1988). I found evidence that the ability of male thornbills to produce independent young improved dramatically as a result of prior breeding experience first during the nestling period and subsequently during the post-fledging period. Male thornbills appear to take three years to become fully competent at raising young because although males usually gain some experience of caring for nestlings in their first year most are unlikely to gain any experience at caring for fledglings until their second.

Avian predators, such as the pied currawong *Strepera graculina*, are the principal cause of nestling and fledgling mortality in brown thornbills (Chapter 2). Experimental studies have found that begging, which increases with hunger, can increase the risk of predation (Haskell 1994, Leech and Leonard 1997). The higher predation rates on nestlings and fledglings provisioned by young male thornbills may arise, therefore, because they are fed less and consequently beg more than young fed by older males. However, since the condition of a brood was not affected by male age, it appears unlikely that higher begging rates are the cause of elevated predation rates at nests provisioned by one-year-old males. Alternatively, the positive relationship between male age and reproductive success in brown thornbills may

arise because young males are less skilled at detecting predators, more conspicuous when visiting the nest, and less effective at leading fledglings away from danger, than older males. Although several studies have found that the ability of males to raise nestlings to fledging improves with age (eg. McCleery and Perrins 1988, Daunt et al. 1999), the only other species where the proportion of fledglings that survive to independence has been shown to improve with parental age is the European bee-eater *Merops apiaster* (Lessells and Krebs 1989).

Pair-bond duration and reproductive performance of brown thornbills

Some studies have found that breeding performance may improve, not simply as a result of experience gained as an individual, but also as a consequence of prior experience of breeding with the same partner (eg. Bradley et al. 1990, Wooler et al. 1990, Emslie et al. 1992). The improved breeding performance is thought to occur principally because established pairs are better able to coordinate their parental duties (for a review see Fowler 1995). I found no evidence that breeding performance was improved by repeatedly breeding with the same partner in the brown thornbill. Pair-bond duration has also been found to have no effect on the breeding performance of several other small passerines (eg. splendid fairy-wrens, Russell and Rowley 1996; European blackbirds, Desrochers and Magrath 1996, indigo buntings *Passerina cyanea*, Payne and Payne 1996, great tits, Dhondt et al. 1996; but see McCleery and Perrins 1985)

In conclusion, the evidence from this study suggests that the reproductive performance of brown thornbills improves with age as a direct result of age-related improvement in the ability of individuals. Male thornbills appear to need to breed for two years before they possess the skills necessary to raise a high proportion of their young to independence. In their first year males gain experience at delivering food to the nest without attracting predators, while in the second they gain additional experience at caring for fledglings. In contrast, female performance improves between only the first and second year as one-year-old birds, that may be in worse condition as a result of dispersal, initiate their first clutch later than older birds and

are less likely to re-nest if a breeding attempt fails. Reproductive success in this species is, as a consequence, influenced more by male than female age.

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Chapter 4

Post-fledging care, philopatry, and recruitment in brown thornbills

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Summary

(1). We describe patterns of post-fledging care, dispersal, and recruitment in four cohorts of brown thornbills *Acanthiza pusilla*. We examine what factors influence post-fledging survival and determine how post-fledging care and the timing of dispersal influence the probability of recruitment in this small, pair breeding, Australian passerine.

(2). Fledgling thornbills were dependent on their parents for approximately 6 weeks. Male fledglings were more likely than female fledglings to survive until independence. For both sexes, the probability of reaching independence increased as nestling weight increased and was higher for nestlings that fledged later in the season.

(3). The timing of dispersal by juvenile thornbills was bimodal. Juveniles either dispersed by the end of the breeding season or remained on their natal territory into the autumn and winter. Juveniles that delayed dispersal were four times more likely to recruit into the local breeding population than juveniles that dispersed early.

(4). Delayed dispersal was advantageous because individuals that remained on their natal territory suffered little mortality and tended to disperse only when a local vacancy was available. Consequently, the risk of mortality associated with obtaining a breeding vacancy using this dispersal strategy was low.

(5). Males, the more philopatric sex, were far more likely than females to delay dispersal. Despite the apparent advantages of prolonged natal philopatry, however, only 54% of pairs that raised male fledglings to independence had sons that postponed dispersal, and most of these philopatric sons gained vacancies before their parents bred again. Consequently, few sons have the opportunity to help their parents. Constraints on delayed dispersal therefore appear to play a major role in the evolution of pair-breeding in the brown thornbill.

Introduction

For many species of birds and mammals, much of the variance in lifetime reproductive success among females can be attributed to differences in the survival of their offspring until recruitment (Clutton-Brock 1988, Newton 1989). Factors that influence offspring survival until recruitment are therefore likely to play a major role in the evolution of life history traits. Consequently, studies examining what factors influence survival both during the period that offspring are dependent on their parents, and from independence until recruitment, are important in understanding the adaptive significance of variation in life history traits among species.

Juvenile survival is frequently related positively to nestling weight or condition in birds (eg. Perrins 1965, Magrath 1991), and birth weight in mammals (eg. Clutton-Brock, Albon & Guinness 1988). This pattern may arise because body mass or condition has a direct affect on juvenile survival. For instance, heavy individuals may be better able to cope with short periods of food shortage than light individuals, or mass may affect dominance and hence the ability to access resources (Perrins 1965, Garnett 1981). Alternatively, size-dependent survival may arise indirectly, as differences in parental or territory quality affect both the size, and the subsequent survival, of juveniles.

The timing of breeding also often influences juvenile survival (reviewed by Daan et al. 1988). In single-brooded species of birds, or mammals that reproduce only once a year, the probability that a juvenile survives to independence frequently declines as the breeding season progresses (eg. Perrins 1970, Guinness, Clutton-Brock & Albon 1978). Juvenile survival may decline because of reduced food availability or because older, more experienced, females breed earlier in the year (Daan et al. 1988, Reiter, Panken & LeBoeuf 1981). However, in multi-brooded birds and in mammals that produce multiple litters in a year seasonal variation in juvenile survival is often less pronounced (eg. Ringsby, Sæther & Solberg 1998).

There is now a considerable amount of information on dispersal patterns in birds and mammals (Greenwood 1980, Clarke, Sæther & Røskaft 1997, Paradis et al. 1998). Evolutionary interpretations focus on either, the female-biased dispersal of birds and the male-biased dispersal of mammals (Greenwood 1980, Dobson 1982, Waser & Jones 1983, Pusey 1987), or delayed dispersal and group-living in the young of cooperative breeders (Emlen 1982, Stacey & Ligon 1987, 1991). Less attention has been paid to intra-sexual variation in dispersal behaviour, and how different dispersal strategies influence the probability of recruitment. However, there is some evidence that hatch or birth dates (Nilsson 1989), dominance status (Hanski, Peltonen & Kaski 1991, Ellsworth & Belthoff 1999), natal territory quality (Newton & Marquiss 1983, Komdeur 1992), and population density (Nilsson 1989, Hanski et al. 1991) may influence individual dispersal in both birds and mammals

In this paper we examine juvenile survival and dispersal in the brown thornbill (*Acanthiza pusilla* (White), Acanthizidae), a small, pair-breeding, passerine, endemic to Australia. The endemic Australian passerines (Corvida) have life histories typified by small clutch sizes, long breeding seasons with multiple nesting attempts, an extended period of post-fledging care, high juvenile survival, and high adult survival (Rowley & Russell 1991). Parental care during the post-fledging period may be more important than nestling weight or the timing of breeding in explaining variation in juvenile survival and recruitment in species with these life history traits. Cooperative breeding is also far more prevalent among the Corvida than the Passerida, the well-studied Northern Hemisphere passerines (Russell 1989), and is thought to be the ancestral trait for some genera within this clade (eg. *Aphelocoma*, Peterson & Burt 1992; *Acanthiza*, Nicholls et al. 2000). Cockburn (1996) has suggested that while prolonged philopatry may be advantageous to juveniles in both cooperative and non-cooperative species in the Corvida, the costs of juvenile retention to adults may sometimes result in the evolution of pair-breeding. In this study, we therefore aimed to: (1) examine what factors influence post-fledging survival to independence, (2) evaluate what prompts the

dispersal of juveniles, and (3) investigate how post-fledging care and the timing of dispersal influence the probability of recruitment in brown thornbills. We also discuss the implications of our results for life history evolution in the Corvida.

Methods

Study species and population

The brown thornbill is a small (ca. 7g) passerine that is common in the eucalypt forests and woodlands of south-east Australia (Blakers, Davies & Reilly 1984). Males are larger and heavier than females (Chapter 2). We studied a colour-banded population of brown thornbills in and adjacent to the Australian National Botanic Garden in Canberra, Australia, between July 1995 and August 1999. The vegetation in the 40 ha Botanic Gardens consists of both plantations of Australian native plants, and natural woodland that is contiguous with a large area (ca. 9 km^2) of dry sclerophyll forest in Canberra Nature Park. Brown thornbills bred both in the Garden and in the adjacent reserve. Approximately 30 pairs maintained permanent territories in the 80 ha study area. Pairs defended small (ca. 2 ha) territories year round. Females laid up to three clutches (98% of clutches contained 3 eggs) but rarely fledged more than one brood during a breeding season that extended form late July (mid-winter) to December (early summer). Females built nests and incubated without assistance, but males contributed to nest defence and the provisioning of nestlings and fledglings.

We monitored the study population throughout the year. During the non-breeding season (January to June) we visited the study area at least once a month to census pairs and associated young, to determine when colour banded juveniles gained a breeding vacancy or new birds entered the population, and to document adult mortality. During the breeding season we monitored pairs at least three times a week to ensure that we documented all nesting attempts even if they failed during incubation (73% of nests were found before laying was completed, n = 173). Hatching and fledging dates were determined by daily visits to the nest towards the end of the nestling period, respectively.

The number of young fledging was estimated as the number banded less the number known to have died before fledging. If the nest was damaged or found empty before the expected fledging date, only those seen alive were assumed to have fledged. Chapter 2 provides additional details about the study area and study population.

Nestling age and status

Nestlings were usually aged to within a day as nests were checked daily between 0700 and 1000 around the time of hatching. The few broods that were found when parents were provisioning nestlings, or that hatched prior to the routine daily visits were aged by comparing their plumage with the plumage of nestlings of known age.

Most clutches hatched synchronously (68%; Chapter 2). Where the clutch did not all hatch on the same day, we identified the younger nestlings at the time of banding using plumage development. We classified nestlings as being either early hatched young, if they hatched before or on the same day as their brood mates, or late hatched young.

Nestling sex, mass, and condition

We sexed all nestlings using a simple PCR-based molecular technique (see Griffiths et al. 1998 for details of the method) using DNA extracted from a small blood sample (ca. 40μl) taken from the brachial vein. Nestlings were usually weighed, banded and bled when they were 6-9 days. In 1997 and 1998, nestlings were also weighed when they were 11-12 days. For these nestlings we also measured wing-length, from the carpal joint to the tip of the longest primary, to the nearest mm. To control for differences in the age at which nestlings were weighed we fitted separate logistic growth curves to both male and female nestlings (male nestling mass = 8.15 / (1+ exp[-0.48 (age - 5.1)]), r^2= 0.84, n = 204; female nestling mass = 7.51 / (1+ exp[-0.39 (age - 4.5)]), r^2= 0.80, n = 185) and used the residuals from these growth curves as an estimate of the relative mass of each nestling. We estimated the condition for those nestlings weighed

and measured when 12 days old using the residuals from the weight-wing length regression (mass = 3.93 + [0.11 x wing], n = 78, r^2= 0.13, $p < 0.001$).

Post-fledging care, juvenile survival, and the timing of dispersal

We conducted focal observations on 38 fledglings (24 broods) produced by 19 females in order to determine the duration of parental care, and to examine factors influencing provisioning rate during the fledgling period. Focal observations were conducted between mid-September and early January in 1996/97 and 1997/98. Observations, which were conducted at weekly intervals, began when fledglings were 2 weeks old and ended when fledglings were either no longer resident on their natal territory or had reached 8 weeks of age. All observations took place between 0900-1200 and 1400-1700 and lasted for 30 minutes. During focal observations we counted the number of times that a fledgling was fed and the identity of the parent providing each food item. To determine whether parental aggression prompted dispersal we also recorded the number of times the focal fledgling was displaced or chased by either parent during the 30 minute focal observation.

Individual nestlings appeared to be fed predominantly by only one of their parents. We therefore conducted additional focal observations, in both 1996 and 1997, to determine which parent was provisioning a further 8 fledglings (4 broods). Each fledgling was observed on two occasions, separated by at least two days, when they were 3 - 4 weeks old. These focal observations lasted for between 20 and 30 minutes.

We monitored the survival of all colour-banded young that were known to have fledged (n = 159) until they reached nutritional independence at six weeks (see Results) using weekly censuses that commenced when fledglings were two weeks old. No fledglings of 2-6 weeks that were missed in a census were ever subsequently found to have been alive. If a fledgling disappeared from their natal territory after six weeks we assumed they had dispersed rather than died. The timing of dispersal for those fledglings that survived to independence was determined either from the weekly

censuses conducted during the breeding season or from the monthly censuses conducted from January until the start of the following breeding season in late July.

Recruitment outside the study area

We attempted to locate colour-banded brown thornbills that had dispersed from our study area by conducting systematic searches outside the study area. Searches were conducted during the autumn and winter (April-June) following each of the four breeding seasons. We searched all suitable habitat within 3 km of the study area in 1996, 1997, and 1998, and all habitat within 0.5 km of the study area in 1995. In each year, we split the area to be searched into blocks of approximately 25 ha and located thornbills by walking any available trail through each block, and walking along every ridge and gully within each block. Blocks were searched once per year. All thornbills located visually or by call (15-30/block) were examined for bands. Observers conducting systematic searches for other species in Canberra Nature Park also occasionally located banded birds. We relocated all the banded individuals found during any of these searches at the start of the next breeding season (August) to confirm that they had survived long enough to enter the breeding population. Additional non-systematic searches were conducted throughout Canberra by volunteers from the Canberra Ornithologists Group without locating any additional banded birds. The number of territories that individuals traversed to obtain a vacancy was estimated by dividing the straight line distance travelled from the centre of their natal territory by the mean diameter of a brown thornbill territory in natural bushland (ca. 160 m).

Statistical analysis

Our data examining juvenile survival and dispersal were structured and not independent as individual fledglings often had siblings that had been raised in either the same brood or other broods produced by their parents. We therefore analysed our data using mixed models incorporating both random and fixed effects (Bennington & Thayne

1994), with 'pair identity' being specified as a random factor in all models. A new pair was considered to have formed when either member was replaced following a death or divorce. We also tested whether there was any evidence of dependency at the brood level by specifying 'brood identity' as an additional random factor in all mixed models. We found that there was little variance associated with 'brood identity': the standard error of the estimate for the variance component was always large compared to the estimate, so 'brood identity' was not included as a random factor in our models.

Models were fitted using Genstat 5.4 for Windows (Genstat 1993). Continuous dependent variables were analysed using the restricted maximum likelihood (REML) procedure, while dichotomous dependent variables were analysed using the generalised linear mixed modelling (GLMM) procedure. When fitting models using either the REML or GLMM procedure we initially fitted a full model with all explanatory variables and their interaction terms. A final model was selected by progressively eliminating non-significant interaction terms, and then non-significant main effects until only significant terms remained. In the case of non-significant main effects the statistics presented refer to the results of dropping the term of interest from the final model plus the non-significant term. When examining continuous dependent variables the significance of a term was determined using the change in deviance when the term was dropped from the model. In contrast, when analysing dichotomous variables the significance of a term was determined using the Wald statistic for that term when it was the last to be entered in a model (see Genstat 1993 for rationale). In all analyses residual plots and normal probability plots were used to examine for unequal variance and deviations from normality among residuals. Natural log transformations were applied to feeding rate and dispersal distance data so that they conformed to the assumptions of the mixed models. Model predictions in the text are presented with either standard errors or the average standard error of differences (s.e.d.).

Results

Post-fledging care

Individual fledglings were usually fed almost entirely by one of their parents (44 of 46 fledglings; 25/26 broods), either because females re-nested and males consequently cared for all fledglings (9 fledglings; 8 broods), a single parent cared for all fledglings (8 fledglings; 5 broods) or broods were divided with each parent providing more than 90% of all food delivered to individual fledglings (27 fledglings; 12 broods). Where broods were divided, males and females were as likely to take care of sons as they were daughters (males: 11 sons/6 daughters, females: 8 sons/10 daughters; χ^2_1= 1.5, p = 0.22).

Fledglings were dependent on their parents for food until they were 6 week old (Fig. 1). The amount of food received by a fledgling began to decline when they were 5 week s old, although they continued to be fed at a low rate for a further 3 weeks (age effect: $\chi^2_6 = 266$, $p < 0.0001$). Post-fledging feeding rates also declined across the breeding season (date effect: $\chi^2_1 = 8.1$, $p = 0.004$) and were affected by the number of fledglings in a parents care (REML model predictions: one fledgling, ln [Total feeds + 1] = 1.86, two or more fledglings, ln [Total feeds + 1] = 1.63, s.e.d. = 0.08; workload effect: $\chi^2_1 = 7.3$, $p = 0.007$). Male thornbills tended to feed their fledglings at a higher rate than females (REML model predictions: males, ln [Total feeds + 1] = 1.79, females, ln [Total feeds + 1] = 1.64, s.e.d. = 0.09; parent effect: $\chi^2_1 = 2.9$, $p = 0.09$). Post-fledging feeding rates were not affected by the sex of the fledgling, the location of the territory (watered plantation or natural woodland), the time of day the focal observation was conducted, or the year of the study (all $p > 0.10$).

Juvenile thornbills began to disperse when between 6 and 7 weeks old. None of the 38 fledglings that were the subject of focal observations disappeared from their natal territory between the ages of 2 and 6 weeks, but 50 % had disappeared by 8 weeks (see sample sizes in Fig. 1). There was little evidence to suggest that dispersal was prompted by an increase in parental aggression. Males were occasionally observed to chase

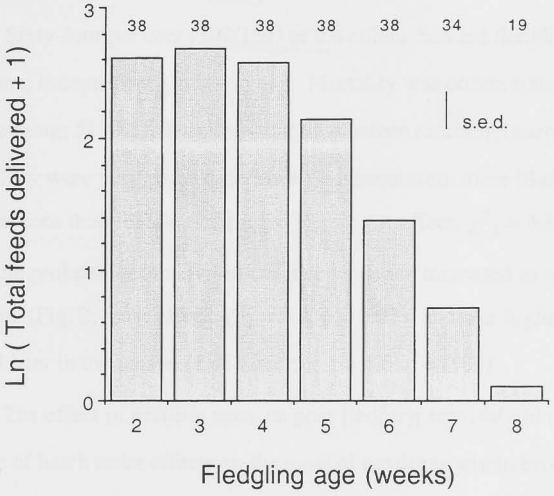

Figure 1. Relationship between fledgling age and the amount of food delivered by their parents per 30 minute focal observation. Bars show the predicted means from the REML model controlling for fledging date and the number of fledglings provisioned by the parent providing care. The line shows the average standard error of differences (s.e.d.).

fledglings when fledglings were 6-8 weeks (n = 5 cases). However, these chases were short and only directed at fledglings that, either repeatedly harassed them for food, or approached a subsequent nesting attempt. Females were never observed to behave aggressively towards fledglings.

Survival to independence

Sixty-four per cent (102/159) of the colour-banded fledglings survived to nutritional independence at six weeks. Mortality was concentrated in the first few days after fledging; 51 of 57 fledglings that died before reaching independence disappeared before they were two weeks old. Male fledglings were more likely to survive to independence than female fledglings (Fig. 2; sex effect: $\chi^2_1 = 4.8$, $p = 0.03$). For both sexes, the probability of surviving to independence increased as nestling weight increased (Fig. 2; mass effect: $\chi^2_1 = 6.2$, $p = 0.03$), and was higher for nestlings that fledged later in the season (date effect: $\chi^2_1 = 4.6$, $p = 0.03$).

The effect of nestling mass on post-fledging survival did not arise simply because of hatch order effects on the mass of nestlings within broods (REML model predictions: mass residuals of early-hatched nestlings = 0.02 g, late-hatched nestlings = 0.08 g, s.e.d = 0.08; $\chi^2_1 = 1.9$, $p = 0.17$). Furthermore, hatch order had no effect on post-fledging survival to independence after controlling for sex, mass, and fledging date (GLMM model predictions: early-hatched nestlings = 0.63 ± 0.05, late-hatched nestlings = 0.71 ± 0.11; hatch order effect: $\chi^2_1 = 1.0$, $p = 0.32$). The number of young fledged, the location of the territory, and the year of the study also had no effect on survival to independence (all $p > 0.10$).

Timing of dispersal

Natal dispersal was bimodal: juvenile thornbills either dispersed early and left their natal territory by the end of February, or delayed dispersal and remained in their natal territory into the autumn and winter (Fig. 3a). Males were far more likely to delay

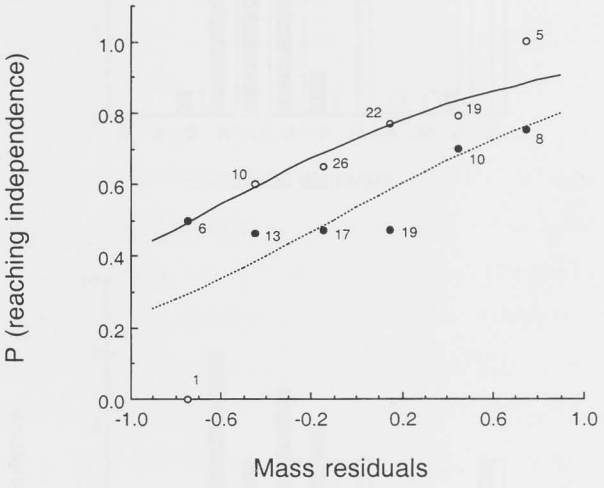

Figure 2. Relationship between the standardised nestling mass of male and female fledglings and post-fledging survival until independence at six weeks. Nestling mass was standardised using the residuals from sex specific logistic-growth curves. Lines show predictions from GLMM models controlling for fledging date (males-plain line; females-dashed line). Points show mean probabilities of reaching independence at 0.3 g intervals with associated sample sizes (males - open circles; females - closed circles).

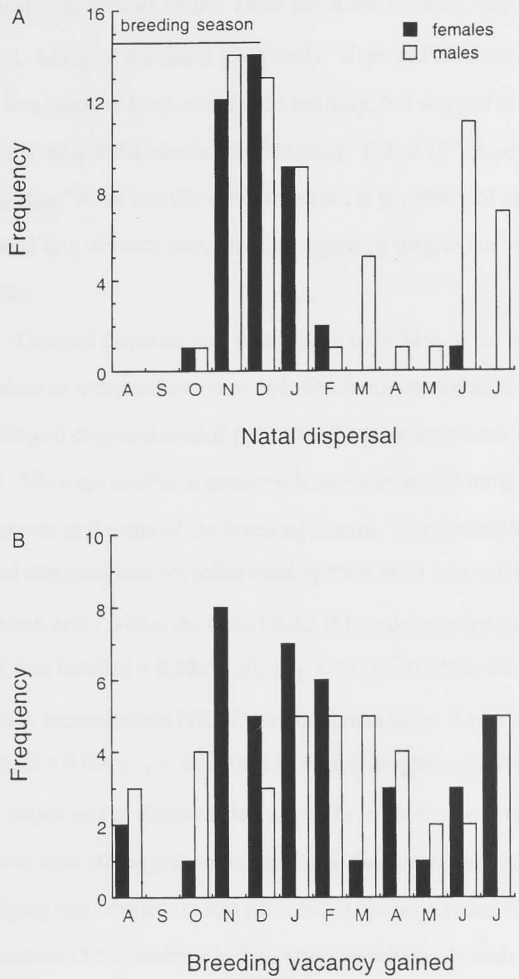

Figure 3. Frequency distributions showing (a) the timing of natal dispersal of fledglings raised in the study population, and (b) the time that breeding vacancies are taken up in the study area. Filled bars are females, open bars are males.

dispersal than females (males 25/63 juveniles, females 1/39 juveniles; $\chi^2_1 = 17.6$, $p < 0.0001$). Many of the males that finally "dispersed" in June and July did not attempt to move to a vacancy in an established territory, but stopped associating with their parents and acquired a small territory by "budding" (12 of 18 "dispersers"). Territories formed by "budding" were initially established at the periphery of the male's natal territory but expanded into territory previously occupied by neighbours if an immigrant female joined the male.

Delayed dispersal was observed in only 54% of territories where one or more son was raised to independence (n = 46). Furthermore, a maximum of one male juvenile ever delayed dispersal even if pairs raised two or more sons to independence (n = 17 cases). We were unable to predict which males would remain in their natal territory and not disperse at the end of the breeding season. The probability that a male juvenile delayed dispersal was not influenced by their mass as a nestling ($\chi^2_1 = 0.0$, $p = 1.0$), their hatch order within the brood (GLMM model predictions: early-hatched = 0.39 ± 0.08, late hatched = 0.44± 0.20; $\chi^2_1 = 0.1$, $p = 0.75$) or the number of male siblings present at independence (GLMM model predictions: 0 sibs = 0.48± 0.11, one or more sib = 0.32 ± 0.09; $\chi^2_1 = 1.8$, $p = 0.18$) suggesting that intra-brood dominance does not play a major role in dispersal decisions. In territories with two or more juvenile males there was also no suggestion that the male that stayed was heavier than his siblings prior to fledging (the heavier sib stayed in 6 of 11 cases, Signed-rank test = 3.5, $p = 0.78$). The location of the territory had no effect on whether a male delayed dispersal (GLMM model predictions: watered plantation = 0.40 ± 0.12; natural woodland = 0.39 ± 0.09; $\chi^2_1 = 0.1$, $p = 0.75$). The date or year a juvenile fledged, the sex or workload of the parent that had provided care, and the density of adult males in the study area at the end of the breeding season also had no effect on whether a male delayed dispersal (all $p > 0.1$).

Juvenile recruitment

Juvenile females were most likely to gain a breeding vacancy in the study area between November and February, when they filled vacancies left by adult females that had died during the breeding season, and between late-June and early-August, when they joined juvenile males that had established new territories by budding (Fig. 3b). The majority of females that settled within the study area originated from outside the study area (40/42 females). In contrast, very few of the male juveniles that settled within the study area came from outside the study area (6/38). There was also less variation in the timing of male recruitment as vacancies resulting from mortality early in the breeding season could be filled by young males from the previous year that had obtained a territory but had failed to attract a mate, while vacancies later in the year were filled by juveniles that had hatched earlier in the same breeding season (Fig. 3b).

Forty-six percent (29/63) of the male fledglings and 21% (8/39) of the female fledglings that were known to have survived until independence were found to gain a breeding vacancy either inside or outside the study area. Male and female juveniles differed in the distance that they travelled to obtain a breeding vacancy (Fig. 4; sex effect: $\chi^2_1 = 21.2$, $p < 0.0001$). Males moved 0-900 m (median distance = 1 territory) while females moved 600-2000 m (median distance = 7 territories). Systematic searches for juveniles were conducted in all habitat within 3 km of the study area so we are likely to have located all male recruits, but may have failed to locate a small proportion of the female recruits. Recruitment and dispersal distances of females may therefore be underestimated.

The distance both male and female juveniles moved to obtain a vacancy was dependent on the dispersal strategy used: juveniles that dispersed early travelled significantly further to gain a breeding vacancy (males: early = 2.4 ± 0.7 territories, n = 8, late = 1.3 ± 0.2, n = 21; females: early = 7.9 ± 1.2, n = 7, late = 4, n = 1; timing of dispersal effect: $\chi^2_1 = 9.1$, $p = 0.003$). The date or year a juvenile fledged, their mass as a nestling or hatch order within a brood, the number of siblings raised to independence,

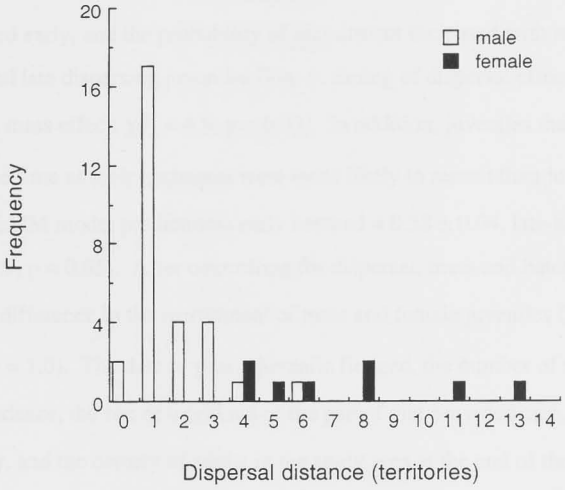

Figure 4. Frequency distribution showing male and female natal dispersal distances (territories traversed) in brown thornbills.

the sex or workload of the parent that cared for them, and the location of the territory all had no affect on how far they travelled to gain a breeding vacancy (all $p > 0.10$).

The probability that a juvenile thornbill gained a breeding vacancy and lived to breed for the first time was influenced by three factors: the time that they dispersed from their natal territory, their weight as a nestling, and the order they hatched within a brood. Juveniles that delayed dispersal were four times more likely to recruit than juveniles that dispersed early, and the probability of recruitment increased with nestling mass for both early and late dispersing juveniles (Fig. 5; timing of dispersal effect: $\chi^2_1 = 22.2$, $p < 0.0001$; mass effect: $\chi^2_1 = 4.9$, $p = 0.03$). In addition, juveniles that hatched early or at the same time as their nestmates were more likely to recruit than juveniles that hatched late (GLMM model predictions: early hatched = 0.38 ± 0.04, late-hatched = 0.16 ± 0.07; $\chi^2_1 = 3.9$, $p = 0.05$). After controlling for dispersal, mass and hatch order effects, there was no difference in the recruitment of male and female juveniles (Fig. 5; sex effect: $\chi^2_1 = 0.0$, $p = 1.0$). The date or year a juvenile fledged, the number of fledglings raised to independence, the sex or workload of the parent that provided care, the location of the territory, and the density of adults in the study area at the end of the breeding season all had no affect on juvenile recruitment (all $p > 0.25$).

Nestling mass and recruitment

During the course of this study 23% (37/159) of the young that were known to have fledged recruited into the local breeding population. We found that males were more likely to recruit than females, and that for both sexes, the probability of recruitment increased as nestling weight increased (Fig. 6; sex effect: $\chi^2_1 = 9.3$, $p = 0.002$; mass effect: $\chi^2_1 = 8.7$, $p = 0.003$). Although hatch order had an effect on juvenile survival between independence and recruitment, hatch order did not have a significant effect on the probability a fledgling was recruited (GLMM model predictions controlling for sex and mass effects: early-hatched = 0.22 ± 0.04, late-hatched = 0.13 ± 0.07, $\chi^2_1 = 1.0$, $p = 0.32$). The date or year a nestling fledged, the number of fledglings in a brood, and the

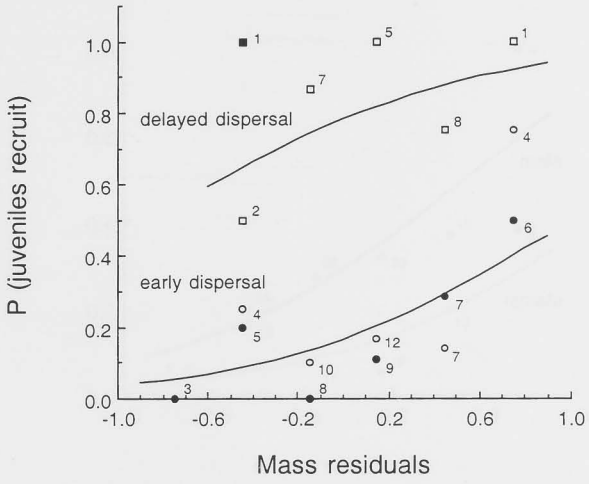

Figure 5. Relationship between the standardised nestling mass of male and female thornbills and the probability that independent young recruit into the breeding population. Nestling mass was standardised using the residuals from sex specific logistic-growth curves. Lines show predictions from GLMM models controlling for hatch order within the brood. Points show mean probabilities of recruitment at 0.3 g intervals for males (open symbols) and females (filled symbols) with associated sample sizes (early dispersal - circles, delayed dispersal - squares).

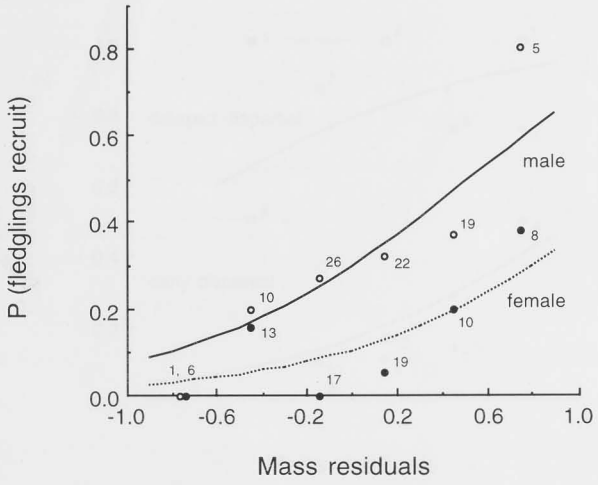

Figure 6. Relationship between the standardised nestling mass of male and female fledglings and their probability of recruiting into the breeding population. Nestling mass was standardised using the residuals from sex specific logistic-growth curves. Lines show predictions from GLMM models (males-plain line; females-dashed line). Points show mean probabilities of reaching independence at 0.3 g intervals with associated sample sizes (males - open circles; females - closed circles).

location of the territory all had no affect on the probability that a fledgling would gain a breeding vacancy (all $p > 0.25$).

Discussion

We found that brown thornbills vary in their dispersal strategy. Females tended to disperse early whereas males either dispersed at the end of the breeding season or postponed dispersal and attempted to fill local vacancies when they became available. Juveniles that delayed dispersal suffered little mortality and were significantly more likely to gain a breeding vacancy in the local breeding population. This study demonstrates that delayed dispersal is not a strategy confined to species that breed cooperatively and suggests that prolonged philopatry may be associated with direct fitness benefits to offspring in both non-cooperative and cooperative species of Corvida. Despite the apparent advantages of delayed dispersal however, only half the pairs of brown thornbills that produced independent young retained offspring on their territory. Most of these philopatric sons gained vacancies before their parents bred again. As a result, few juvenile thornbills have the opportunity to help their parents. Constraints on delayed dispersal therefore appear to play a major role in the evolution of pair-breeding in the brown thornbill.

Post-fledging survival

Post-fledging survival to independence of brown thornbills was influenced by their mass as a nestling, the date on which they fledged, and their sex. This is the first study to demonstrate that post-fledging survival of an Australian endemic passerine improves with nestling mass, although several studies on passerines from the Northern hemisphere have found that the probability of surviving to independence is related to nestling body mass or body condition (eg. dunnocks *Prunella modularis* (Linnaeus), Davies 1986; great tits *Parus major* Linnaeus, Perrins 1965, Tinbergen & Boerlijst 1990;

song sparrows *Melospiza melodia* (Wilson), Hochachka & Smith 1991; blackbirds *Turdus merula* Linnaeus, Magrath 1991).

Post-fledging survival may be influenced by nestling mass because heavier individuals are in better condition and are therefore better equipped to cope with short periods without food. We found that heavy thornbill nestlings are also in good condition ($r = 0.93$, $n = 78$, $p < 0.0001$) providing some support for this explanation. In addition, we found that male nestlings are, on average, in better condition than female nestlings (males = 0.29 ± 0.06 g, $n = 44$, females = $- 0.37 \pm 0.07$ g, $n = 34$, ANOVA, $F = 56.8$, d.f. $= 1$, $p < 0.0001$) which may help explain sex differences in post-fledging survival in the brown thornbill. Alternatively, mass and sex effects on post-fledging survival in brown thornbills may both arise because size influences dominance and hence access to resources provided by parents or vulnerability to predation. However, this explanation appears unlikely as we may then have expected other factors that could influence dominance, such as hatch order, to affect survival to independence. Furthermore, sex and nestling mass do not have any effect on the amount of food fledglings obtain form their parents during the nestling period (sex effect: $\chi^2_1 = 0.5$ $p = 0.48$; mass effect: $\chi^2_1 = 0.3$, $p = 0.58$; sex.mass interaction: $\chi^2_1 = 0.4$, $p = 0.53$).

Post-fledging survival in birds is also often influenced by the timing of breeding (Daan et al. 1988). The survival rate of brown thornbill fledglings improved as the season progressed perhaps because environmental conditions improve dramatically between September and December when the average minimum daily temperature rises from 3.1 to 11.2 ^{o}C. Mortality of fledglings was concentrated in the first few days after fledging when they are likely to be most sensitive to environmental conditions, do not fly proficiently, and are consequently vulnerable to predators. Other studies on multi-brooded species have also found that the relationship between fledging date and survival may be positive (Brinkhof et al. 1993, Ringsby et al. 1998). In contrast, in most single-brooded species the survival rate of fledglings decreases as the breeding season progresses (Daan et al. 1988, Sæther 1990).

Juvenile survival to recruitment

The most important factor influencing survival and recruitment of juvenile brown thornbills was the timing of dispersal. Delayed dispersal was advantageous because individuals that remained on their natal territory suffered little mortality and were able to inherit their natal territory (2/26), move into a nearby territory as soon as a vacancy became available (8/26), or acquire a small territory by budding (12/26). Individuals that gained a territory via the latter route could then either attract a mate and expand into territory previously occupied by their neighbours (8/12), or live on their small territory until a local vacancy became available (4/12). Consequently, juveniles that delayed dispersal had a high probability of obtaining a breeding vacancy. Prolonged juvenile philopatry and extended parental investment in retained offspring is linked to fitness benefits in other non-cooperative species of Corvida. For example, male Siberian jays *Perisoreus infaustus* (Linnaeus) that postpone dispersal for a year or more subsequently obtain territories of higher quality, and have higher lifetime reproductive success, than males that disperse in their first summer (Ekman, Bylin & Tegelstrom 1999). The results of our study and the long term study on Siberian jays are important as they demonstrate that delayed dispersal can have fitness benefits for offspring of non-cooperative as well as cooperative species. These results also suggest that delayed dispersal in cooperative species in the Corvida are more likely to be driven by direct fitness benefits to offspring rather than indirect benefits accrued by raising non-descendent kin.

Male thornbills were far more likely than females to delay dispersal and obtain the advantages associated with natal philopatry. This pattern may result because the benefits of early dispersal may be greater for females than males. .However, our data suggest that early dispersing females were no more likely to recruit than early dispersing males (GLMM model predictions: males = 0.17 ± 0.06, females = 0.17 ± 0.06; sex effect: $\chi^2_1 = 0.0$, $p = 1.0$). Furthermore, the date on which early dispersers left their natal territory did not affect the recruitment of either males or females (date effect: $\chi^2_1 = 0.1$,

$p = 0.75$, sex.date interaction: $\chi^2_1 = 0.8$, $p = 0.37$). Alternatively, females may be less likely to delay dispersal because they disperse a greater distance than males and are therefore less likely to benefit from spending the autumn and winter on their natal territory. Female-biased dispersal is extremely common in birds (Greenwood 1980, Clarke et al. 1997). Greenwood (1980) argued that sex biases in dispersal arose because male birds, which often defend resource-based territories, are more likely to benefit from remaining near their natal area, while females will benefit from dispersal as it allows them to assess and choose among males and/or to avoid inbreeding.

Nestling mass also has a significant effect on recruitment in thornbills. This result is surprising since most studies on northern hemisphere passerines, which do not have such an extended period of post-fledging care, find that nestling weight does not influence juvenile survival after young have reached independence (Magrath 1991, but see Sullivan 1989). It is possible that the effect of nestling mass on recruitment arises because parents that produce heavier nestlings also provide better care during the fledgling period. Alternatively, since nestling weight reflects differences in structural size as well as differences in condition in brown thornbills ($r = 0.36$, $n = 78$, $p = 0.001$) larger, heavier, individuals may be dominant to smaller, lighter, individuals and therefore at an advantage when attempting to disperse successfully. This may also explain why hatch order, which often influences dominance in birds (eg. Hahn 1981, Stanback 1994), has a significant effect on recruitment in brown thornbills.

Implications for life history evolution in the Corvida

Small clutch sizes in tropical and Southern Hemisphere birds are argued to have evolved in response to high nest predation rates, which select for reduced parental activity near the nest, and selection for high numbers of renesting attempts (Skutch 1949, Cody 1966, Kulesza 1990). However, predation rates on nestlings can be relatively low in Corvida species (eg: brown thornbill, 4 % per day, Chapter 2; white-browed scrubwren *Sericornis frontalis* (Vigors and Horsfield) 5.3% per day, R. Magrath pers. comm.). Furthermore, many genera within the Corvida have long nesting periods (Ricklefs 1993) which is at odds with the evidence that higher nest predation rates are usually associated with faster nestling development and shorter nesting periods (Martin 1995). Small clutch sizes and an extended nesting period may both be explained by food limitation, since reduced food availability can lead to both small clutch sizes and a long slow developmental period (Lack 1948, 1968, Martin 1987). Our study suggests that there is likely to be a trade-off between the number and the quality of nestlings that a brown thornbill can raise. This implies that small clutch sizes are more likely to have evolved in response to a limited food supply than high predation rates.

Implications for the evolution of pair-breeding in the Acanthiza

Cooperative breeding is likely to be the ancestral trait in the Acanthizidae (Nicholls et al. 2000). In order to understand mating system evolution within this family we therefore need to explain why species such as the brown thornbill have evolved pair-breeding, rather than attributing pair-breeding to some phylogenetic lag. There are no obvious differences in either the life history or ecology of pair-breeding and cooperatively breeding species in the Acanthizidae. Pair-breeding species do not have lower annual survival rates or lower productivity than cooperative species (Chapter 2) and both pair-breeding and cooperative species are found in all habitat types across the entire geographic range of the family (Nicholls et al. 2000). Cockburn (1996) has suggested that while prolonged parental investment and juvenile philopatry may be

advantageous for both cooperative and pair-breeding species in the Corvida, the costs of juvenile retention may sometimes be too great for parents to allow offspring to remain on their natal territory. The retention of juveniles may be costly to parents either because they subsequently compete with adults for opportunities to reproduce (Cockburn 1996), or they depress limiting resources on the natal territory (Koenig et al. 1992). Our study confirms that delayed dispersal is advantageous for juveniles even in a pair-breeding species, but did not find any evidence for conflict between parents and offspring over the timing of dispersal. Nevertheless, no juveniles were retained on 52 % of the territories where one or more juvenile reached independence (n = 54). This suggests that even though delayed dispersal has fitness benefits for both parents and offspring the ability of juveniles to remain on their natal territory is constrained perhaps because food availability on the small permanent territories is limited during the non-breeding season. Juveniles, that are likely to have poor foraging skills compared to their parents, may then be forced to leave their natal territory to obtain sufficient food.

The prevalence of cooperative breeding in the Acanthizidae suggests that for some species there are likely to be fitness benefits associated with both delayed dispersal and helping behaviour. However, while some brown thornbills have the opportunity to help, because they live adjacent to their parents and fail to attract a mate in their first year, they never assist their parents. These males may not help raise young because the fitness benefits associated with conducting forays in search of breeding vacancies in the local area are greater than the fitness benefits of helping. The benefits of helping may be low because young males are unable to increase the reproductive success of their parents. Male brown thornbills breeding as a one-year-old are less likely to fledge young than older males, because they are less proficient at delivering food to the nest without attracting the attention of predators (Chapter 3). Furthermore, help by auxiliary males in a cooperative species from the Acanthizidae, the white-browed scrubwren, was only found to increase reproductive success when females were in their first year (Magrath in press).

In conclusion, we suggest that three factors appear to have influenced the evolution of pair-breeding in brown thornbills. First, few juveniles have the opportunity to delay dispersal and remain on their natal territory despite the advantages associated with natal philopatry. Second, there is a high probability that the few juveniles that do delay dispersal obtain a breeding vacancy, reducing the number that are available to help their parents raise young in subsequent years. Finally, as the individuals that obtain a territory by budding but fail to attract a mate are young males, they may not help because they are more likely to reduce, rather than enhance, the reproductive success of their parents.

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Chapter 5

Mate guarding limits extra-pair paternity in brown thornbills

submitted to Behavioral Ecology

Abstract

We used DNA-fingerprinting and detailed behavioural observations to investigate the role of male-male competition, female mate-choice, and conflict between pair members on patterns of extra-pair paternity in the brown thornbill. Extra- pair paternity was uncommon (6.2% of 178 offspring; 11.9 % of 67 broods) and there was no evidence of intra-specific brood parasitism. Male thornbills ensured paternity in their own broods by guarding their mates closely when they were fertile which enabled them to detect and then evict rival males before they were able to approach the female. Males were solely responsible for the close proximity of partners during the fertile period so mate guarding appears to be a male tactic aimed at preventing female infidelity rather than a cooperative behaviour of the pair aimed at preventing extra-pair copulations and/or female harassment. Females did not attempt to escape male guarding, but given the opportunity would solicit copulations from intruding males. Males that were either small and/or breeding for the first time were more likely to be cuckolded than larger and older males. This pattern may arise because although female thornbills prefer large males as mates, their ability to express this preference is constrained when they are paired to older males. Females paired to small males may be more likely to benefit from extra-pair fertilisations than females paired to large males as large offspring have higher post-fledging survival. Older males are more likely to constrain female choice than yearling males because, although they do not spend more time close to their partners during the fertile period, they respond to intruders more aggressively which could limit opportunities for extra-pair copulations.

Introduction

Despite the prevalence of social monogamy, birds often seek copulations with partners other than their social mates (reviewed in Birkhead and Møller 1992). However, the level of extra-pair paternity varies from 0% in some species (eg. northern fulmars *Fulmarus glacialis*, Hunter et al. 1992) to more than 60 % in others (eg. splendid fairy-wren *Malurus splendens,* Brooker et al. 1990; superb fairy-wren *M. cyaneus*, Mulder et al. 1994). The underlying causes of such variation in extra-pair paternity remain poorly understood despite the proliferation of paternity studies of birds over the last decade (Petrie and Kempenaers 1998).

Factors influencing extra-pair paternity are expected to differ markedly in species where sperm competition is driven by male-male competition rather than female choice (Lifjeld et al. 1994). Early studies emphasised reproductive conflict between males, as they were presumed to be the principal beneficiaries of extra-pair mating (Trivers 1972, McKinney et al. 1984). However, females may also actively pursue extra-pair copulations (eg. black-capped chickadees *Poecile atricapillus* Smith 1988, blue tits *Parus caeruleus*, Kempenaers et al. 1992). Recent studies have therefore focussed on the role of female choice and the benefits females obtain from extra-pair copulations (Birkhead and Møller 1993, Hunter et al. 1993, Kempenaers and Dhondt 1993). Nevertheless, even when females pursue extra-pair copulations, patterns of extra-pair paternity are unlikely to be solely determined by the costs and benefits of these copulations to females as the behaviour of females may be constrained by the actions of their social mate (Petrie and Kempenaers 1998).

The level of extra-pair paternity in a population reflects the outcome of a series of possible conflicts between females, their mates, and one or more extra-pair males (Lifjeld et al. 1994). The conflict between pair and extra-pair males is straightforward as each male will increase their reproductive success by fertilizing the eggs of the female. Pair males are therefore expected to invest in paternity assurance behaviours if they increase their certainty of paternity, but adjust the intensity of these behaviours in

response to changes in the risks of cuckoldry (Birkhead and Møller 1992). Conflicts of interest between females and their mates are dependent on whether extra-pair copulations and extra-pair paternity are costly or beneficial to females. If females suffer from extra-pair copulations, they should cooperate with their mate to reduce the likelihood of extra-pair copulations. However, if a female benefits from extra-pair copulations, her interests and those of her mate will conflict. In this case, male paternity assurance behaviours may be directed more towards preventing their mate from seeking extra-pair copulations rather than simply deterring rival males. Detailed behavioural studies are therefore required to determine the role of the two sexes in influencing the outcome of sperm competition.

Sperm competition has led to the evolution of a variety of male strategies that will reduce the likelihood that they are cuckolded (Birkhead and Møller 1992). The two most common paternity guards in birds are mate-guarding and frequent copulations. Mate guarding has been defined as 'close following of females by their mates during the female's fertile period' (Birkhead and Møller 1992 pp118), a behaviour that may enable males to disrupt extra-pair copulations. In contrast, high copulation rates may function to dilute or displace sperm resulting from successful extra-pair copulations. Other paternity assurance behaviours used by male birds include increased territorial defence (Westneat 1993) and elevated song rates during their mate's fertile period (Grieg-Smith 1982). Both may serve to reduce intrusions by rival males.

In this paper we examine genetic parentage in a population of brown thornbills (*Acanthiza pusilla*; Acanthizidae) to determine the extent of extra-pair paternity in this pair-breeding Australian passerine. We identify two male traits associated with extra-pair paternity and use detailed behavioural observations to investigate the role of female choice, male-male competition, and conflict between pair members in determining paternity.

Methods

Study species and population

The brown thornbill is a small (ca. 7g), yet long-lived (up to 17 year; Baker et al. 1999), passerine that is common in the eucalypt forests and woodlands of south-eastern Australia (Blakers et al. 1984). We studied a colour-banded population of brown thornbills in and adjacent to the Australian National Botanic Garden in Canberra, Australia, between 1995 and 1998. The vegetation in the 40 ha Botanic Gardens consists of both plantations of Australian native plants, and natural woodland that is contiguous with a large area (ca. 9 km^2) of dry sclerophyll forest in Canberra Nature Park. Brown thornbills bred both in the Garden and in the adjacent reserve. We followed the fate of 15 pairs in 1995, and approximately 30 pairs per year between 1996 and 1998. Pairs defended small (ca. 2 ha) territories year round. Females laid up to three clutches (98% of clutches contained 3 eggs) and fledged up to two broods during a breeding season that extended from late July (mid-winter) to December (early summer). Females built the nests and incubated without assistance, but males contributed to nest defence and the provisioning of nestlings and fledglings (Chapter 2).

Field methods

We monitored the study population throughout the year. During the non-breeding season we visited the study area at least once a month to census pairs and associated young, to determine when colour-banded juveniles gained a breeding vacancy or new birds entered the population, and to document adult mortality. During the breeding season we observed pairs at least three times a week to confirm the identity of the social parents, locate nests, and monitor the progress of each nesting attempt.

The majority of birds monitored during the breeding season (> 95% in each year) were banded with an Australian Bird and Bat Banding Scheme aluminium band and a unique combination of 3 coloured bands. Blood samples (10-70μl) were taken from the brachial vein of each adult at the time that they were banded. We measured the mass of

birds to the nearest 0.1g, tarsus and head-bill length to the nearest 0.1mm, and wing and tail length to the nearest 1mm, whenever they were caught.

Female thornbills build small domed nests in grass tussocks or dense shrubs. We determined hatch dates by daily visits to the nest towards the end of the incubation period and/or the appearance and size of nestlings. Nestlings were banded when 6-9 days old. Blood samples (10-60μl) were taken from the brachial vein of all nestlings that survived to banding.

Male age and body size

We categorised breeding males into two age classes ("yearlings" and "older"). Males were of known age if they were banded as nestlings or identified as juveniles on the basis of eye colour when captured for the first time (Rogers et al. 1986). We also assumed that males were yearlings if they traversed more than one territory to fill a vacancy in the study area. Adult males in this study never moved more than one territory following divorce or the death of their mate.

We used scores from the first component of a principal component analysis of three linear size measurements (tarsus, head-bill, and wing) as an index of body size. Mean values for each trait were used when individuals were captured multiple times. PC1 explained 41% of the variation in male size and the respective character loadings for tarsus, head-bill, and wing were 0.71, 0.71, and -0.06.

Behavioural observations

We conducted detailed behavioural observations on a total of 17 pairs of brown thornbills, watching 10 pairs in 1997 and 7 pairs in 1998. Watches on focal pairs started when females began nest building and continued, at two day intervals, until the day the second egg was laid. Watches therefore spanned the period from 18 days before the first egg was laid (day –18) until two days after the first egg was laid (day +2). Eleven of the 17 pairs only initiated one clutch. The remaining six were watched during two breeding

attempts. Focal watches were all conducted between 0900 and 1200, commenced when both members of a pair were located, and lasted for 10 minutes. During each focal watch we recorded: (i) the distance between each member of the pair (< 1 m, 1-5 m, 6-10 m, >10 m) at 30 s intervals, (ii) the number of flights greater than 10 m that each partner made away from their mate, (iii) the number of times an individual followed its partner's flight away within 5 s, and (iv) the number of songs performed by the male during the 10 min observation period. We also noted any copulation attempts or aggressive behaviour between pair males, pair females, and intruding birds. Watches were not conducted if it was raining. We also discarded watches if we lost sight of the female or failed to determine the distance between pairs on ≥80% of the 30-s time intervals.

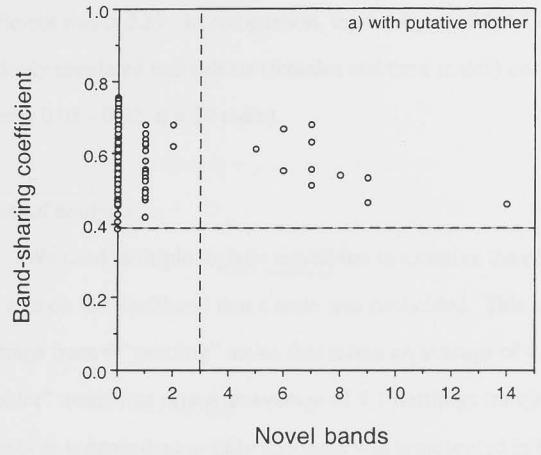
DNA-based sexing and fingerprinting

Adult thornbills can not be reliably sexed from measurements or plumage. We therefore used a polymerase chain reaction (PCR)-based method (Griffiths *et al.* 1998) to sex all putative parents. The results obtained using the molecular technique were always consistent with behavioural evidence that suggests only the female in each pair contributes to incubation (n = 58 pairs).

We used multi-locus DNA fingerprinting to determine the parentage of 178 nestlings from 67 broods produced by 37 pairs between 1995 and 1997. Standard DNA fingerprinting techniques were employed (eg. Bruford et al. 1992). Briefly, DNA was extracted from blood samples using a large-volume phenol-chloroform method, then digested with restriction enzyme *Hae*III (Pharmacia Biotech). Digests (6μg) from 2-3 families were run on 40 cm long, 0.8 % agarose gels in TBE buffer for 75 h at 75 V. Family groups were run in adjacent lanes, with nestlings on either side of their putative parents. Following electrophoresis, DNA was transferred to a nylon membrane (Hybond, Amersham) by Southern blotting. Blots were fixed by baking at 80 ^{o}C for 2 h then hybridized with radioactively labelled minisatellite probe 33.6 (Jeffreys et al. 1985).

Hybridizations were carried in a Hybaid oven; probe was labelled by random priming with 30μCi ^{32}P-dCTP using Ready-To-Go Labelling Beads (Pharmacia Biotech). Following post-hybridization washes in 2xSSC, 0.1% SDS, membranes were exposed to x-ray film (Amersham) for 1-14 days at -70 C, using zero to two intensifying screens, to produce autoradiographs.

We scored fingerprints by marking the presence of all bands on an acetate overlay. The average number of fingerprint bands that could be scored per individual was 21.4 (range 12-33). We compared fingerprints of offspring and putative parents to assess parentage by counting the number of novel bands (bands present in the fingerprint of the offspring but not present in either of their putative parents), and calculating band-sharing coefficients between offspring and each of their putative parents. The band-sharing coefficient was calculated as twice the sum of shared bands divided by the sum of all bands scored in both individuals (Wetton et al. 1987). We considered bands to be different if they were more than 0.5 mm apart or they showed at least a twofold difference in relative intensity. We analysed the distribution of novel fragments in order to distinguish between rare bands arising from mutation and those attributable to extra-pair parentage. In this study the mutation rate was calculated as being 0.0079 per band per meiotic event which is comparable to that of other passerine species (eg. Westneat 1990, Chuang et al. 1999). The probability of an offspring having one, two, or three novel bands as a result of mutation is therefore 0.169, 0.029, and 0.005 respectively. Offspring with three or more novel bands are therefore unlikely to have acquired them by mutation, and we considered these offspring to be unrelated to one or both of their putative parents. We then used band-sharing coefficients to determine if excluded offspring were related to either their putative mother or their putative father (Fig 1). An excluded offspring was considered to be unrelated to a parent if their band-sharing coefficient was lower than 0.39, the lowest band sharing coefficient observed between mothers and non-excluded offspring (Fig. 1a). In the few cases where we had a sample of DNA from the putative father but not the putative mother (8 nestlings from 3 broods



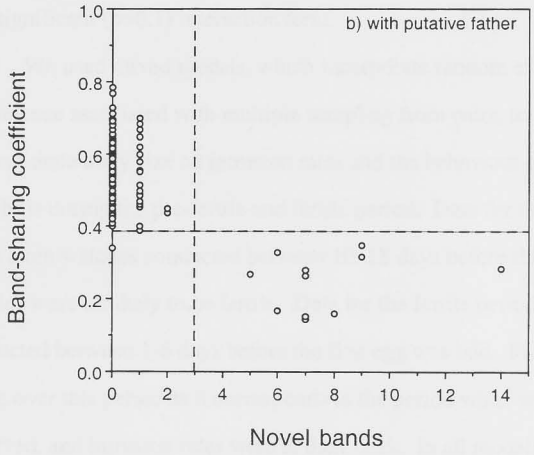


Figure 1. Relationship between the number of novel bands present in offspring and band-sharing coefficients with a) their putative mother, and b) their putative father.

produced by 3 pairs) we assigned paternity to the putative father if their band-sharing coefficient was > 0.39. In comparison, the background level of band-sharing between putatively unrelated individuals (females and their mates) averaged 0.20 ± 0.08 S.D. (range = 0.08 - 0.32, n = 37 pairs).

Statistical analysis

We used multiple logistic regression to examine the effect of male age and male body size on the likelihood that a male was cuckolded. This analysis used data on parentage from 6 "yearling" males that raised an average of 4.0 nestlings (range 3-6) and 27 "older" males that raised an average of 4.1 nestlings (range 3-9). We treated the two data sets as independent as only one male was represented in both age classes. The significance of the two main effects were assessed using the change of deviance calculated when dropping the term of interest from the model after the removal of the non-significant ($p>0.1$) interaction term.

We used mixed models, which incorporate random effects to account for dependence associated with multiple sampling from pairs, to examine the effect of male age and male body size on intrusion rates and the behaviour of male and female thornbills during the pre-fertile and fertile period. Data for the pre-fertile period were taken from watches conducted between 10–18 days before the first egg was laid, when females were unlikely to be fertile. Data for the fertile period were taken from watches conducted between 1-6 days before the first egg was laid. Females were assumed to be fertile over this period as it corresponds to the period when within pair copulations were observed, and intrusion rates were at their peak. In all models the pair was treated as a random effect, and the time period, male age, male body size, and the date on which the clutch was subsequently initiated (Jan. 1 = 1) were treated as fixed effects. Mixed models were fitted using the restricted maximum likelihood (REML) procedure in Genstat 5.4 for Windows (Genstat 1993). When fitting models we initially fitted a full model with all explanatory variables and their interaction terms. A final model was

selected by progressively eliminating non-significant interaction terms, and then non-significant main effects until only significant terms remained. In the case of non-significant main effects the statistics presented refer to the results of dropping the term of interest from the final model plus the non-significant term.

In all analyses residual plots and normal probability plots were used to examine for unequal variance and deviations from normality among residuals. Means are presented with standard errors unless otherwise stated.

Results

Parentage analysis

DNA fingerprinting detected no evidence for intra-specific brood parasitism (Fig. 1a), and revealed that only 6.2 % of nestlings (11 of 178), from 11.9% of broods (8 of 67) were unrelated to their putative father (Fig 1b). The proportion of nestlings sired by extra-pair males, and the proportion of broods containing extra-pair young did not vary significantly over the three years of this study (Table 1; G-test: nestlings, $G = 1.67$, $df = 2$, $p > 0.25$; broods, $G = 0.26$, $df = 2$, $p > 0.75$).

The majority of broods (6 of 8) with extra-pair young contained only one illegitimate nestling. The two remaining broods contained two and three extra-pair young, respectively. The number of novel bands shared by the extra-pair young in each of these broods suggests they were sired by a single extra-pair male.

Yearling males were more likely to be cuckolded than older males (Fig 2; age effect: $\chi^2_1 = 4.2$, $p = 0.04$). Controlling for age, small males were also more likely to be cuckolded than large males (Fig. 2; size effect: $\chi^2_1 = 4.3$, $p = 0.04$; age.size interaction: $\chi^2_1 = 0.0$, $p = 0.96$). Overall, 22% of males (7 of 32) were cuckolded on at least one occasion.

Table 1. Summary of extra-pair paternity data for brown thornbills between 1995 and 1997.

	1995	1996	1997	Total
% of extra-pair offspring (N)	5.3 (34)	9.2 (65)	4.0 (75)	6.2 (178)
% of broods with extra-pair young (N)	15.4 (13)	12.5 (24)	10.0 (30)	11.9 (67)
% of males cuckolded (N)	16.2 (12)	15.0 (20)	13.0 (23)	21.9 (32)

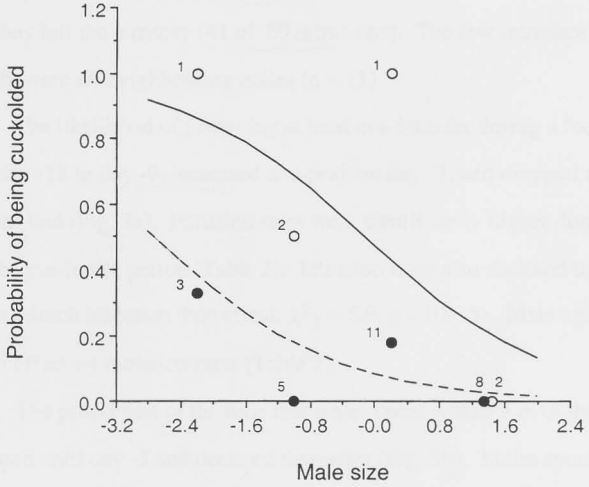


Figure 2. The effect of male body size (PC1) and male age class (yearling and older) on the probability a male is cuckolded. The curves show the results of the logistic regression: yearlings are the plain line, older males are the dashed line. Points depict actual probabilities for 1.2 unit categories and associated sample sizes: yearling males are open circles, older males are filled circles.

Intrusion rates, and mate-guarding behaviour

We observed a total of 68 territorial intrusions during the 227 10-min focal watches conducted from day -18 until day 2. Intruding males did not advertise their presence, but were usually detected by the resident male before they were able to approach within one metre of the female. Resident males always flew directly at intruders to force them away from the female, and frequently continued to chase them until they left the territory (41 of 69 intrusions). The few intruders we were able to identify were all neighbouring males (n = 11).

The likelihood of observing at least one intruder during a focal watch was low from day -18 to day -9, increased to a peak on day -3, and dropped again when the first egg was laid (Fig. 3a). Intrusion rates were significantly higher during the fertile period than the pre-fertile period (Table 2). Intrusion rates also declined through the breeding season (clutch initiation date effect: $\chi^2_1 = 5.9$, $p = 0.015$). Male age and male body size had no effect on intrusion rates (Table 2)

The proportion of the time that males spent within 5 m of their mates also increased until day -3 and declined thereafter (Fig. 3b). Males spent approximately twice as much time within 5 m of their mate during her fertile period than during pre-fertile period (Table 2). Male age and male body size had no affect on the proportion of time males were within 5 m of their mate (Table 2). There was also no seasonal variation in the proportion of time males spent close to their mate (clutch initiation date effect: $\chi^2_1 = 0.11$, $p = 0.74$).

The close proximity of partners during the fertile period was a consequence of male rather than female behaviour. Males were more likely to follow their mate when she moved away during the fertile period than during the pre-fertile period (Table 2). In contrast, the proportion of male flights away that the female followed within 5 s was no different in the pre-fertile and fertile periods (Table 2). Male age and body size had no affect on either the proportion of female flights that males followed or the proportion of male flights that females followed (Table 2).

Table 2. Summary of the effect of male age (yearling and older) and body size (PC1) on intrusion rates and the behaviour of brown thornbills in the pre-fertile and fertile periods.

Data presented are means ± S.E. Measures include the proportion of time that pairs are less than 5 m apart, the number of flights of greater than 10 m each sex make away from the other, and the proportion of their partners flights that they follow within 5 seconds. Statistics refer to results of REML models. The proportion of male flights that females follow was not examined statistically as the majority of females (10 of 17) never followed their mate in either the pre-fertile or fertile period

	Yearling males (N= 6)		Older males (N= 11)		Period		Age class		Body size	
	Pre-fertile	Fertile	Pre-fertile	Fertile	χ^2_1	p	χ^2_1	p	χ^2_1	p
Intrusion rate (per h)	1.7 ± 0.5	3.7 ± 1.0	0.9 ± 0.3	2.8 ± 0.6	**7.7**	**0.006**	1.1	0.29	0.12	0.73
Prop. time <5m apart	0.31 ± 0.05	0.61 ± 0.06	0.30 ± 0.04	0.52 ± 0.03	**24.0**	**0.000**	0.46	0.50	1.8	0.18
Male										
Song rate / h	22.9 ± 7.4	11.3 ± 5.3	17.5 ± 4.7	15.0 ± 3.4	1.5	0.22	0.25	0.62	1.2	0.27
Flights away / h	1.4 ± 0.3	3.3 ± 0.7	3.3 ± 0.6	5.2 ± 0.8	**9.3**	**0.002**	**6.1**	**0.01**	2.2	0.14
Prop. flights followed	0.44 ± 0.13	0.87 ± 0.08	0.55 ± 0.08	0.85 ± 0.09	**10.4**	**0.001**	1.0	0.32	0.29	0.59
Female										
Flights away / h	7.6 ± 0.8	7.8 ± 1.05	5.5 ± 1.1	7.2 ± 0.9	1.2	0.0.27	3.6	0.06	1.7	0.19
Prop. flights followed	0.05 ± 0.05	0	0.21 ± 0.07	0.07 ± 0.05	-	-	-	-	-	-

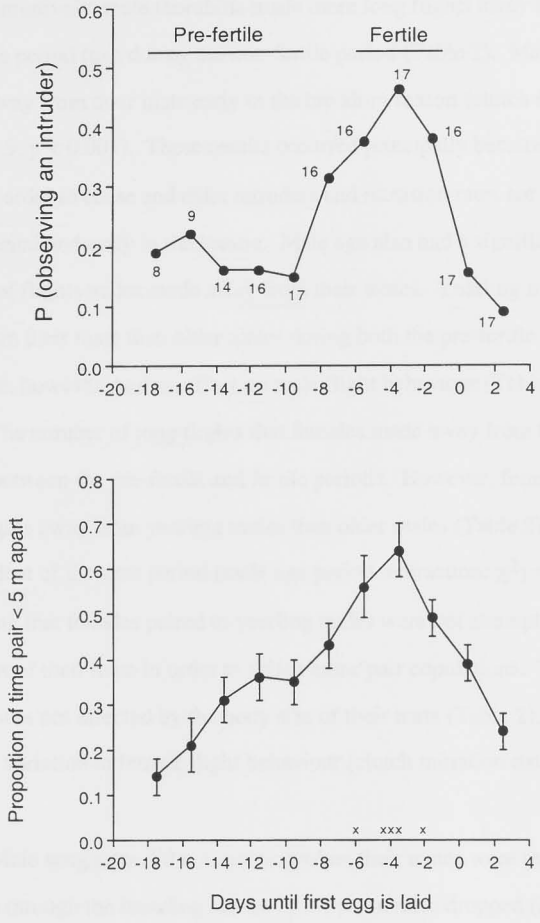


Figure 3. Relationship between the number of days remaining until the first egg was laid and a) the likelihood of observing an intruder during a 10 minute focal watch, and b) the proportion of time that pair members were within 5 m of one another ± S.E. The crosses in (b) show when within-pair copulations were observed. Points depict values for two-day periods starting on day –18 and are placed at the mid-point of each period. If pairs were watched on more than one occasion in a time period, the mean of the watches was used. The number of pairs observed during each period is shown adjacent to the points in (a).

Counterintuitively, male thornbills made more long flights away from their mate during the fertile period than during the non-fertile period (Table 2). Males also made more flights away from their mate early in the breeding season (clutch initiation date effect: $\chi^2_1 = 11.9$, $p < 0.001$). These results occurred principally because males leave their mates in order to chase and evict intruders and intrusion rates are higher both during the fertile period and early in the season. Male age also had a significant effect on the number of flights males made away from their mates. Yearling males made less flights away from their mate than older males during both the pre-fertile and fertile periods. Male size, however, had no affect on male flight behaviour (Table 2).

The number of long flights that females made away from their mate did not change between the pre-fertile and fertile periods. However, females tended to make more flights away from yearling males than older males (Table 2). This effect was independent of the time period (male age.period interaction: $\chi^2_1 = 0.70$, $p = 0.40$) suggesting that females paired to yearling males were not attempting to escape the attentions of their mate in order to solicit extra-pair copulations. The flight behaviour of females was not affected by the body size of their mate (Table 2). There was also no seasonal variation in female flight behaviour (clutch initiation date effect: $\chi^2_1 = 0.72$, $p = 0.40$).

Male song rates did not increase when their mates were fertile (Table 2) or decrease through the breeding season as intrusion rates dropped (clutch initiation date effect: $\chi^2_1 = 0.20$, $p = 0.65$). Male age and body size also had no affect on male song rates (Table 2).

We observed 5 within-pair copulations (Fig 3b). All were solicited by the female. No extra-pair copulations were observed. However, one female solicited an intruding male before he was chased away by her mate.

Discussion

Although brown thornbills breed exclusively in pairs, males attempt to increase their reproductive success by seeking copulations with females other than their social mate. DNA-fingerprinting revealed, however, that extra-pair paternity was uncommon (6.2 % of offspring, 11.9 % of broods). Nevertheless, this level of extra-pair paternity is fairly typical of pair-breeding birds (Gowaty 1996). The testes mass of brown thornbills (mean = 0.11 g; McLaughlin1992) which is close to that predicted for a 7.3 g bird (Møller 1991) also suggests that the level of sperm competition in this species is comparable with that of other birds.

Extra-pair paternity may result from extra-pair copulations, mate switching, mate replacement or inseminations that occur before social bonds are formed (Moore and McDonald 1993, Pinxten 1993). Extra-pair paternity in this study is likely to have resulted from extra-pair copulations since new pair-bonds were usually established several months prior to breeding and none of the males that were cuckolded were recent arrivals on the territory. Mate switching was rare; occurring only occasionally at the start of the breeding season (n = 4), or following nest failure (n = 2). Moreover, females that switched mates were never observed to initiate a clutch until they had been resident on a territory and apparently paired to a male for at least 17 days. Male brown thornbills were usually replaced rapidly if they died during the breeding season, but mate replacement during or just after the female's fertile period does not account for any of the extra-pair paternity documented in this study. We considered young in two broods fed by replacement males but sired by the males present during the females' fertile period to be legitimate young.

Direct benefits from extra-pair copulations

Female birds may obtain a variety of direct benefits as a result of soliciting extra-pair copulations (Birkhead and Møller 1992). Potential direct benefits include foraging privileges on the territory of the extra-pair male (Gray 1997), paternal investment by the extra-pair male (Gray 1997, Otter et al. 1994), and future mate appraisal (Heg et al.

1993). These direct benefits are unlikely to explain extra-pair copulations in brown thornbills as females do not leave their territory to forage, there is no parental investment by extra-pair males, and divorce rates are extremely low (unpublished data).

Another possible direct benefit is fertility assurance (McKinney et al. 1984, Wetton and Parkin 1991, Krokene et al. 1998). There is some evidence to suggest that fertility assurance may play a role in explaining why female brown thornbills solicit extra-pair copulations . The female thornbill that produced an entire brood of extra-pair young may have had a sterile or incompatible partner as she subsequently laid a second clutch containing three eggs that all failed to hatch. Krokene et al. (1998) point out that the risk of laying an infertile clutch need not be high for females to benefit from performing a few insurance copulations with extra-pair males. The rate of total loss of paternity found here for brown thornbills (1.5%, 1/67) is comparable with the rate documented in studies of blue and great tit populations (1.2 to 3.6%; Krokene et al. 1998). In the study conducted by Krokene et al. (1998), however, many broods (27 to 36%) contained at least some extra-pair young and there were no phenotypic correlates of extra-pair mating success. In brown thornbills extra-pair paternity rates were lower, although 23% (n = 35) of females cuckolded their mate on one or more occasion. More importantly, extra-pair paternity was not independent of male phenotype, as small and/or young males were more likely to be cuckolded. If females could predict male fertility because fertility covaries with male phenotype we might expect only females paired to males with phenotypes towards the lower end of the distribution to seek extra-pair copulations (Sheldon 1994). However, we know of no evidence to suggest that functional fertility is linked to structural size in birds, although there is some evidence of a correlation between functional fertility and male age (Hilton 1968, Hill 1994). Moreover, there is little evidence to suggest that the ability of male brown thornbills to fertilise an entire clutch, which only ever contain three eggs, is affected by either their size or their age. In an analysis restricted to broods containing no extra-pair paternity, we found that the probability of one or more eggs in a clutch failing to hatch does not

decline as males either increase in size (GLMM model predictions: male PC1 score of -1, probability of hatch failure = 0.16 + 0.08, male PC1 score of +1, probability = 0.33 + 0.08; $\chi^2_1 = 2.30$, $p = 0.13$) or increase in age (GLMM model predictions: yearling male, probability of hatch failure = 0.33 + 0.22, older male, probability = 0.30 + 0.08; $\chi^2_1 = 0.0$, $p = 1.0$). Factors other than fertility assurance may therefore play a more important role in explaining mating patterns in brown thornbills.

Indirect benefits from extra-pair copulations

We found that small or young males were more likely to be cuckolded than large or old males. Size and age of male have frequently been shown to influence levels of within-pair paternity in birds (Table 3). This association could arise because small young males are perceived by their partner as being of low genetic quality, making the female more likely to seek or accept extra-pair matings (Weatherhead and Boag 1995). Alternatively, large experienced males could be more adept at defending their mates against intruders. Females paired to such males may therefore be unable to obtain extra-pair matings (Wagner et al. 1996). Our data are inadequate to distinguish these hypotheses, but circumstantial evidence suggests that both possibilities warrant further attention.

The genetic quality hypothesis predicts that when males vary in quality it will pay females paired to low quality males to solicit extra-pair copulations from high quality males in an attempt to improve the viability or sexual attractiveness of their young. Female brown thornbills paired to young or small males were the most likely to obtain extra-pair fertilisations. Can male age and male size indicate genetic quality in brown thornbills? Female thornbills might benefit from mating with older males because long-lived males may have genotypes that promote survival and could therefore provide genes that enhance offspring viability (Halliday 1978, Manning 1985, Kokko and Lindstrom 1996). The theoretical basis for this argument remains controversial (Hansen and Price 1995, Kokko 1998). Nevertheless, male age is the most common

phenotypic correlate of extra-pair mating success in birds (Table 3). Female thornbills could also gain an indirect genetic benefit from mating with large males. We lack data on heritability, but juvenile survival from both fledging to independence and from independence to recruitment is related positively to nestling size in brown thornbills (Chapter 4).

Female birds may also gain indirect genetic benefits from extra-pair copulations if extra-pair fertilisations increase the genetic diversity of their brood (Williams 1975, Gavin and Bollinger 1985). However, there is little evidence to suggest that female thornbills routinely attempt to produce broods fathered by multiple males.

Conflicts of interest and extra-pair paternity in brown thornbills

Female brown thornbills had opportunities to solicit extra-pair copulations because extra-pair males made regular visits to the territories of fertile females. There was little evidence that females thornbills regularly visited males on other territories. to obtain extra-pair copulations . Females were never observed outside their territory during the breeding season. However, female thornbills rarely attempted to solicit copulations from intruding males and no successful extra-pair copulations were observed during this study. This suggests that either females are selective about which males are acceptable as extra-pair benefits and few females benefit from extra-pair copulations, or the behaviour of females is constrained by the actions of their mate.

Males thornbills attempted to minimise paternity loss to extra-pair males by guarding their mates assiduously when their mates are fertile and intrusion rates are high. Males that were close to their mate were always able to detect rival males. Males, upon detecting an intruder, frequently pursued and actively evicted them from their territory. Extra-pair males were therefore rarely able to approach the female. Mate-guarding by close following has been found to be the main paternity guard employed by males in most other territorial passerine species (Birkhead and Møller 1992). Female thornbills made no attempt to facilitate male mate-guarding. Females did not reduce the number of

Table 3. Summary of studies that have identified male traits associated with paternity gained within or outside the pairbond. All traits identified, with the exception of those indicated by an asterisk, are positively associated with paternity. Studies which do not identify a trait associated with either within-pair or extra-pair paternity are denoted with a dash.

		Male trait that influences:		
Species		within-pair paternity	extra-pair paternity	Reference
Acanthiza pusilla	brown thornbill	age, size (PC1)	-	this study
Acrocephalus arundinaceus	great reed warbler	-	song (repertoire)	Hasselquist et al. 1996
Agelaius phoeniceus	red-winged blackbird	-	age, longevity	Weatherhead & Boag 1995
Dendroica petechia	yellow warbler	size (PC1)	plumage streaking	Yezerinac & Weatherhead 1997
Dolichonyx oryzivorus	bobolink	age	-	Bollinger & Gavin 1991
Emberiza citrinella	yellowhammer	-	age, plumage colour	Sundberg & Dixon 1996
Ficedula albicollis	collared flycatcher	forehead patch width, wing patch size	forehead patch width	Sheldon & Ellegren 1999
Hirundo rustica	barn swallow	tail length	-	Smith et al. 1991
		tail length	-	Moller & Tegelstrom 1997
		tail length, (song rate)	-	Moller et al. 1998
		tail length	tail length	Saino et al. 1997
Ictera galbula bullockii	Bullock's oriole	age	age	Richardson & Burke 1999
Malurus cyaneus	superb fairy-wren	age	moult date	Dunn & Cockburn 1999
Malurus splendens	splendid fairy-wren	age	-	Brooker et al. 1990

Table 3 ctd.

Species		Male trait that influences: within-pair paternity	extra-pair paternity	Reference
Panurus biarmicus	bearded tit	beard length	-	Hoi & Hoi-Leitner 1997
Parus caeruleus	blue tit	song (strophe length)	age, size (tarsus), song (strophe length)	Kempenaers et al. 1997
Parus cristatus	crested tit	condition	-	Lens et al. 1997
Passer domesticus	house sparrow	-	age	Wetton et al. 1995
Passserina cyanea	indigo bunting	age	-	Westneat 1987
		age*	-	Westneat 1990
Phylloscopus trochilus	willow warbler	condition	-	Bjornstad & Lifjeld 1997
Progne subis	purple martin	age	age	Morton et al. 1990,
		age, size	age	Wagner et al. 1996
Setophaga ruticilla	American redstart	age	age	Perrault et al. 1997
Sialia sialis	eastern bluebird	age	-	Gowaty & Bridges 1991
Zonotrichia leucophrys	white-crowned sparrow	age*	-	Sherman & Morton 1988

flights that took them away from their mate, or increase the number of male flights that they followed during their fertile period compared to their pre-fertile period. Mate guarding therefore seems to be a male tactic directed towards preventing female infidelity, rather than a cooperative behaviour of the pair aimed at preventing extra-pair copulations and/or female harassment.

Mate guarding has been shown experimentally to be an effective paternity guard in birds (Komdeur et al. 1999). However, studies that have combined observational data with paternity analysis have found no consistent relationship between mate-guarding and extra-pair paternity. Males that invest more in mate-guarding may be either more (eg. blue tits, Kempenaers et al. 1995; eastern bluebirds, Gowaty and Bridges 1991) or less likely to be cuckolded (eg. bluethroats, Krokene et al. 1996, dunnocks *Prunella modularis* Burke et al. 1989). We found no evidence to suggest that large males or old males spent more time close to their partner when they were fertile than small or young males. However, old males made more flights away from their mate during both the pre-fertile and fertile period than yearling males. We believe this is because old males are more aggressive than yearling males when faced with a rival male. Old males are more likely to pursue intruders until they leave the territory than yearling males (proportion of intrusions resulting in long chases: yearlings = 0.50 ± 0.10, older males = 0.77 ± 0.08, $t_{13} = 2.10$, $p = 0.06$). Old males may therefore be less likely to be cuckolded than yearling males because they respond to intruders more aggressively which could reduce the number of opportunities females have to copulate with a high quality extra-pair male.

In summary DNA-fingerprinting has revealed low levels of extra-pair paternity in the brown thornbill. Extra-pair fertilisations appear to be rare because (i) male thornbills stay close to their mates when they are fertile and are usually able to evict rival males before females have the opportunity to solicit extra-pair copulations, and (ii) female thornbills do not attempt to escape close guarding by their mate. However, female thornbills that are given the opportunity will occasionally solicit copulations from

intruding males. Females paired to males that were either small and/or breeding for the first time were more likely to obtain extra-pair fertilisations than females paired to large older males. We suggest that this pattern occurs because female thornbills prefer large males as mates, but that the opportunity to express this preference is constrained when females are paired to an older male. Females paired to small males may be more likely to benefit from extra-pair fertilisations than females paired to large males as large offspring have higher post-fledging survival (Chapter 4). Short term detention experiments that increase the opportunity for females to obtain extra-pair copulations, and allow characteristics of pair males and extra-pair males solicited by females to be compared, would enable our hypothesis to be tested and shed light on the function of extra-pair paternity in brown thornbills.

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Chapter 6

Costly sons drive sex ratio variation in the brown thornbill

Abstract

Females should adjust the sex ratio of their offspring in response to the fitness costs and benefits accrued through sons and daughters. However, there is scant experimental evidence that sex ratio biases observed in wild bird populations provide fitness benefits to females. I investigated sex ratio variation in the brown thornbill, a sexually dimorphic Australian passerine. Female thornbills in new pairs produced female-biased broods while females in established pairs produced male-biased broods. I evaluated the fitness consequences of this pattern by manipulating the sex ratio of broods provisioned by new and established pairs. Although sons have higher energy requirements than daughters, the increased costs of raising sons are confined to females in new pairs. The costs of raising sons differ for females in new and established pairs because males in new pairs provision at a lower rate than males in established pairs and male thornbills do not adjust their feeding rates in response to the sex ratio of the brood. Females in new pairs with male-biased broods are therefore forced to provision at a higher rate and yet still produce nestlings that are in relatively poor condition and consequently unlikely to obtain a breeding vacancy. Female brown thornbills therefore obtain fitness benefits from adjusting the sex ratio of their offspring in response to the level of resources provided by their partner.

Theory suggests that parents should vary their level of investment in sons and daughters in response to the fitness costs and benefits accrued through male and female offspring (Frank 1990). One way individuals may vary their total investment in each sex is to modify the sex ratio of offspring produced. In contrast to invertebrates, adaptive modification of sex ratios appears uncommon in birds and mammals. Nevertheless, recent studies demonstrate that birds and mammals may adjust sex ratios in ways that appear to be adaptive (Hardy 1997, Sheldon 1998). For example, birds produce biased sex ratios when the reproductive value of sons/and or daughters varies with laying date (Dijkstra et al. 1990), resource availability (Appleby et al. 1997), territory quality (Komdeur et al. 1997), female condition (Nager et al. 1999), or male attractiveness (Ellegren et al. 1996, Sheldon et al. 1999).

Parents can also vary their investment in sons and daughters by modifying the level of care they provide in relation to the sex of each young or the sex ratio of their brood. This may occur when the energetic needs of the two sexes differ or when sons and daughters have different effects on parental fitness after independence as a consequence of sex-biased dispersal (Stamps 1990, Clark 1978, Malcolm and Marten 1982). Sex biases in resource allocation have been widely documented in mammals that are dimorphic in size, where sons appear to have higher energy requirements than daughters, or where offspring of one sex are more likely to compete with or help parents in future breeding attempts (reviewed by Clutton-Brock 1991). In contrast, sex-biased provisioning has been documented in only a few species of birds (reviewed by Leonard et al. 1994), although laboratory studies on dimorphic species have found that the energy intake of the larger sex is higher than that of the smaller sex (Fiala and Congdon 1983, Teather and Weatherhead 1988, Anderson et al. 1993). In both mammals and birds where sex-biased provisioning has been reported it is often unclear whether the observed differences in provisioning are an adaptive parental strategy or a response to differences in the behaviour of sons and daughters (Clutton-Brock 1991). However, recently it has been demonstrated that the feeding rates of male reed warblers (*Acrocephalus orientalis and A. arundinaceus*) increased with the proportion of sons in the brood, but not with brood size, suggesting that

fathers preferentially invest in sons rather than respond to the energetic demands of the brood (Nishiumi et al. 1996, Westerdahl et al. 2000).

Despite the proliferation of studies on avian sex allocation patterns over the last decade, prompted by advances in molecular techniques that allow nestlings to be sexed before substantial mortality has occurred, experimental evidence for adaptive allocation strategies in birds remains limited (Sheldon 1998). Experiments have been used to provide compelling evidence that facultative manipulation of primary sex ratios in response to a variety of factors is possible in birds (eg. Komdeur et al. 1997, Kilner 1988, Sheldon et al. 1999) but have rarely been used to investigate the fitness consequences to parents and offspring of particular allocation strategies (but see Komdeur 1998, Nager et al. 1999, 2000). In this paper I report the results of a four year study that used both natural data, and an experiment where sex ratio was manipulated early in the nestling period, to investigate sex ratio variation and parental provisioning behaviour in the brown thornbill (*Acanthiza pusilla*).

Brown thornbills have a number of life-history traits that are expected to influence an individuals sex allocation strategy. First they are sexually dimorphic in body size (males are 14 % heavier than females, Chapter 2). Furthermore, sex differences in body mass arise early in the nestling period (Chapter 4). Second, nestling condition has a significant influence on juvenile survival and recruitment to the breeding population in both males and females (Chapter 4). Third, variance in male reproductive success is likely to be higher than female reproductive as a result of extra-pair paternity (Chapter 5). Finally, 98% of clutches contain three eggs (Chapter 2) so females do not adjust the number of offspring they produce in response to resource availability. Where sons are more expensive to raise than daughters the reproductive costs of producing sons may be dependent on the level of resources available to parents (Gomendio et al. 1990). Under these conditions female thornbills with access to fewer resources would be expected to produce female-biased broods whereas females with access to more resources would be expected to produce male-biased broods. In addition, Burley (1981) has suggested that where parental traits associated with paternal attractiveness are heritable and

sons benefit more from these traits than daughters it may be adaptive for females to adjust the sex ratio of their offspring in response to these traits. Previous work suggests that female thornbills may prefer to mate with large males (Chapter 5). If body size is heritable in brown thornbills pairs with large parents would therefore be expected to produce male-biased broods, whereas pairs with small parents would be expected to produce female-biased broods.

In this study I use observations of natural broods of known sex ratio and experimental manipulated all-male and all female broods to determine food allocation strategies of males and females. I demonstrate that male nestlings appear to have higher energy requirement than female nestlings. I also examine sex ratio variation in the brown thornbill and use experimental manipulations of brood sex ratio to show that the observed sex ratio biases are likely to have fitness benefits for parents.

Methods

Study species and population

The brown thornbill is a small, yet long-lived (up to 17 years), passerine that is common in the eucalypt forests and woodlands of south-eastern Australia (Blakers et al. 1984, Baker et al. 1999). Males are larger and heavier than females (mean body mass: males = 7.3 g, females = 6.4 g; Chapter 2). I studied a colour-banded population of brown thornbills in and adjacent to the Australian National Botanic Garden in Canberra, Australia, between 1995 and 1998. The vegetation in the 40 ha Botanic Gardens consists of both plantations of Australian native plants, and natural woodland that is contiguous with a large area (ca. 9 km^2) of dry sclerophyll forest in Canberra Nature Park. Brown thornbills bred both in the Garden and in the adjacent reserve. I followed the fate of 15 pairs in 1995, and approximately 30 pairs per year between 1996 and 1998. Pairs defended small (ca. 2 ha) territories year round. Females laid up to three clutches but rarely fledged more than one brood during a breeding season that extended from late July (mid-winter) to December (early summer). Females started to incubate after they had laid the final egg in a clutch.

Eggs hatched synchronously approximately 18 days later. Females built nests and incubated without assistance, but males helped provision nestlings and fledglings (Chapter 2).

Field methods

I monitored the study population throughout the year. During the non-breeding season (January to June) I visited the study area at least once a month to census pairs and associated young, and to determine when colour banded juveniles gained a breeding vacancy or new birds entered the population. During the breeding season I observed pairs at least three times a week to confirm the identity of the social parents, locate nests, and monitor the progress of each nesting attempt. The majority of birds monitored during the breeding season (> 95% in each year) were banded with an Australian Bird and Bat Banding Scheme aluminium band and a unique combination of 3 coloured bands. I located nests by watching females when they were nest-building, following females back to their nests during incubation, or watching adults feed nestlings (73% of nests were found before egg-laying was completed, n = 173). I determined hatch dates by daily visits to the nest towards the end of the incubation period and/or the appearance and size of nestlings. I banded, weighed, and collected a blood sample (10-40μl) from nestlings when they were 6-9 days old. In 1997 and 1998, I also re-weighed nestlings when they were 10-12 days old.

I conducted feeding watches on a total of 31 complete (ie. 3 chick) broods produced by 25 pairs to examine factors influencing the amount of food delivered to nestlings and the feeding rates of male and female thornbills. Watches were conducted between mid August and early December in 1996, 1997, and 1998. Watches on 12 broods began when nestlings were 1-2 days old and continued, at 2-day intervals, until the broods fledged (n = 11) or were taken by a predator (n = 1). Watches on the remaining 19 broods began when nestlings were 9-10 days old and continued, at 2-day intervals, while nestlings remained in the nest. All watches took place between 0900-1200 or 1400-1700 and lasted 30 minutes. During focal watches

I counted the number of times each parent visited the nest with food. There was little obvious variation in the size of the deliveries made to the nest. Watches were not conducted if it was raining and were abandoned if either parent became agitated by our presence. Abandoned watches were attempted again later in the day if time allowed, with the observer sited further from the nest.

Pair-bond duration, age, and body size

Pairs were classified as being either new pairs if they were breeding together for the first time, or established pairs if they had bred together in a previous year of the study. Adults were classified as being either yearlings or older. Adults were known to be yearlings when breeding in the study area for the first time if they had been banded either as a nestling or as a juvenile. Juvenile brown thornbills have brown eyes whereas those of an adult are red (Rogers et al. 1986). Since juveniles attain adult characteristics after only 3-4 months I also assumed that adults were yearlings if they traversed more than one territory to fill a vacancy in the study area. Adults in this study never moved more than one territory following divorce or the death of their mate.

I used scores from the first component of a principal component analysis of three linear size measurements (tarsus, head-bill, and wing) as an index of body size. Separate analyses were conducted for male and female thornbills. Mean values for each trait were used when individuals were captured multiple times. PC1 explained 41% of the variation in male size and 50% of the variation in female size. The respective character loadings for tarsus, head-bill, and wing were 0.71, 0.71, and –0.06 for males, and 0.71, 0.66, and 0.20 for females.

Sexing of adults and offspring

It is not possible to sex brown thornbill adults or nestlings using morphological measurements or plumage. I therefore determined the sex of all parents and offspring using a DNA-based test that relies on PCR amplification of a section of the CHD1 genes (CHD1-W and CHD1-Z) located on the avian sex

chromosomes (see Griffiths et al. 1998 for details of the method). The DNA used to sex individuals was isolated from blood samples using either a chelex extraction or a standard phenol/chloroform extraction. Molecular sexing always confirmed the gender of adults sexed using behavioural cues (n = 58 pairs). Nestlings that subsequently obtained vacancies in the study area were also always sexed correctly (n = 28 males, n = 1 female).

Brood sex ratio manipulation

I manipulated the sex ratio of broods provisioned by 6 new pairs and 4 established pairs in 1998 by transferring chicks between broods when they were 6-7 days old. Chicks had been sexed on the day prior to being transferred using DNA extracted from the blood sample collected at banding. I created a total of 5 all-male and 5 all-female broods. Each brood contained three chicks, and the chicks in each brood had hatched within 24 hours of one another. The brood size of experimental pairs was held constant. All experimental broods contained both foster chicks and chicks that had not been transferred. Nests used in this experiment had, wherever possible, been surrounded by wire-mesh cages prior to hatching to reduce the likelihood of predation. These cages did not appear to have any affect on adult behaviour. I weighed nestlings to 0.1 g using a Pesola balance both at the start of the experiment and 4 days later when nestlings were 11 days old. Nestlings were always weighed between 0800 and 0900. I used changes in the residuals from sex-specific growth curves to determine how nestling condition changed during the course of the experiment. I conducted feeding watches at experimental nests when nestlings were 10, 12 and 14 days old. All watches took place between 0900-1200 or 1400-1700 and lasted 60 minutes. During focal watches I counted the number of times each parent visited the nest with food. I attempted to catch adults provisioning experimental broods using a single mist net situated near the nest when nestlings were 13 days old. Mist-nets were in place for a maximum of 60 minutes. I used the residuals from sex-specific regressions between body mass and body size (PC1 score) to estimate the condition of any adult captured.

Statistical analysis

I carried out analyses with a statistical modelling approach using Genstat 5.4 for Windows (Genstat 1993). The data collected during this study were rarely independent as pairs provisioned 1-2 broods and were watched between 3 and 16 times, females produced between 1 and 6 clutches, and broods contained 3 nestlings. I therefore used mixed models, which incorporate random effects to account for dependence associated with multiple sampling to examine parental provisioning behaviour, brood sex ratios, and changes in nestling condition during the brood manipulation experiment.

I examined the behaviour of pairs provisioning unmanipulated broods by fitting separate linear mixed models to three dependent variables: the total number of deliveries per hour, male deliveries per hour, and female deliveries per hour. I fitted the models using the restricted maximum likelihood (REML) procedure in Genstat, with "pair" specified as a random term. Explanatory variables considered were year, hatch date (Jan. 1 = 1), time (am/pm), sex ratio (male-biased/female-biased), territory type (natural woodland or watered plantation), male age/status (yearling male, older male in a new pair, older male in an established pair), and female age/status (yearling female, older female in a new pair, older female in an established pair). A composite variable was used to examine how age and pair status affected male and female delivery rates as the two variables are not independent (a yearling has to be in a new pair). When fitting the models I initially fitted a full model that contained all explanatory variables of interest and all two-way interaction terms. A final model was selected by progressively eliminating non-significant interaction terms ($p > 0.1$), and then non-significant main effects until only significant terms remained. The significance of terms was assessed using the change in deviance (which approximates to a χ^2 distribution) associated with dropping that term from a fuller model.

I examined variation in brood sex ratios by fitting a generalised linear mixed model with binomial errors and a logit link using the GLMM procedure in Genstat.

In this model "female" was specified as a random term, the number of males in a brood was used as the response variable and brood size at banding was used as the binomial denominator. Explanatory variables were assessed in two stages as there was more information available for some variables than for others. I first fitted a model that contained "data quality" (entire clutch sampled/ part clutch unsampled), hatch date, year, territory type, and both male and female body size as explanatory variables, and included all two-way interaction terms. I reduced the number of variables in the initial model by progressively eliminating non-significant interaction terms ($p > 0.1$) and then non-significant main effects. The significance of terms was assessed using the Wald statistics (which have a similar distribution to χ^2) calculated when the term of interest was fitted last in the model. All interaction terms and main effects were eliminated. I subsequently examined the effect of male age, female age and pair-bond duration on brood sex ratio. Since these variables are inter-related their effects were first assessed by fitting a mixed model with a single composite variable ("age/pair-bond duration"). This variable classified pairs into 5 types: yearling male/yearling female, older male/yearling female, yearling male/older female, older male/older male in a new pair, and older male/older female in an established pair. I confirmed the results of this model by fitting a second model where each variable was assessed after controlling for the other two. Restricting the model to broods where the entire clutch was sexed does not alter the statistical significance or interpretation of the results.

I also used mixed models to examine male and female feeding rates, and changes in nestling condition between 7 and 11 days of age, at experimental broods. These models were fitted using the REML procedure described previously, with "pair" specified as a random term. Explanatory variables considered were pair status (new or established pair), experimental treatment (male or female broods), nestling age (10, 12, and 14 days), type of chick (foster or biological), hatch date, time of day, and territory type. I again initially fitted a full model that contained all the explanatory variables of interest and two-way interactions, and selected a final model

by progressively eliminating non-significant interaction terms ($p > 0.1$) and then non-significant main effects.

I used a two-way analysis of variance to examine, separately, the condition of male and female thornbills from new and established pairs after they had provisioned either all-male or all-female broods for 6 days. In these analyses pair status and experimental treatment were treated as factors, and their interaction term was included in the model.

In all analyses residual plots and normal probability plots were used to examine for unequal variance and deviations from normality among residuals. Feeding rates to natural broods were log transformed so that they conformed to the assumptions of the mixed models. Model predictions are presented as means ± the standard error, or means with the least significant difference (l.s.d.) which is equal to twice the overall average standard error of differences. Brood sex ratios throughout the paper refer to the proportion of a brood that are male.

Results

Parental provisioning behaviour

The total number of food deliveries per hour that parents made to a nest increased with nestling age (Fig. 1; age effect, $\chi^2_7 = 133.1$, $p < 0.0001$). Male-biased broods were also fed significantly more than female biased-broods (Fig. 1; sex ratio effect, $\chi^2_1 = 12.7$, $p = 0.0004$). Total delivery rates varied from year to year and across the day, being higher in 1996 than in 1997 or 1998 (year effect, $\chi^2_2 = 24.1$, $p < 0.0001$) and in the morning compared to the afternoon (time of day effect, $\chi^2_1 = 3.9$, $p = 0.05$). Total delivery rates were not affected by the hatch date of a brood (date effect, $\chi^2_1 = 0.4$, $p = 0.53$) or the location of the territory (territory type effect, $\chi^2_1 = 0.9$, $p = 0.34$).

Female delivery rates increased with nestling age and were higher in 1996 than in 1997 or 1998 (Table 1). Females also fed male-biased broods more than female biased broods (Fig 2a, Table 1). Female age and pair status had no effect on female delivery rates (Fig. 2a, Table 1). The hatch date of the brood, the time of the

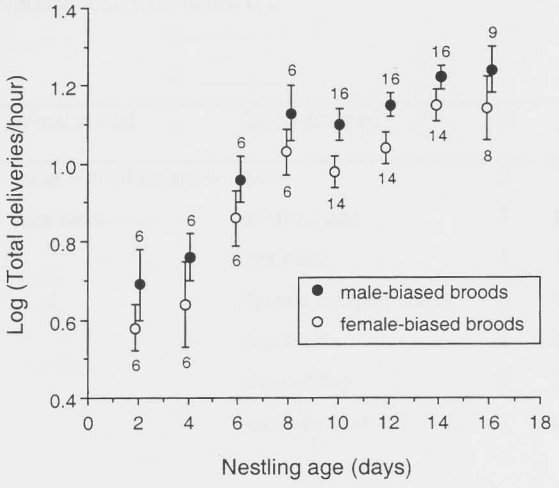

Figure 1. Relationship between nestling age and the total number of feeding deliveries made by parents to unmanipulated nests with female-biased (open circles) or male-biased (filled circles) broods. Broods all contained three nestlings. Means are presented with standard errors. Numbers above or below the points refer to the number of male or female-biased broods observed at each nestling age.

Table 1. Summary of analysis of female and male provisioning rates at unmanipulated three-chick broods of known sex ratio, modelled using the REML procedure. Pair was specified as a random term in both mixed models. For clarity of presentation, P values are only reported if they are below 0.1.

	Final model	Term dropped	df	χ^2	P
Females	year + nestling age + sex ratio	year	2	23.6	< 0.0001
		nestling age	7	88.5	< 0.0001
		sex ratio	1	10.1	< 0.001
		female age/pair status	2	0.7	NS
		hatch date	1	0.1	NS
		time of day	1	2.6	NS
		territory type	1	0.3	NS
Males	year + nestling age + male age/pair status	year	2	19.6	< 0.0001
		nestling age	7	121.2	< 0.0001
		male age/pair status	2	10.6	< 0.001
		sex ratio	1	0.0	NS
		hatch date	1	0.2	NS
		time of day	1	0.2	NS
		territory type	1	1.7	NS

* P < 0.01, ** P < 0.001, *** P < 0.0001

Figure 2. Relationship between the age and pair status of a) males and b) females and their feeding rates when provisioning unmanipulated nests with female-biased (open bars) or male-biased (filled bars) broods. Bars show REML model predictions for 12 day old nestlings after controlling annual variation in feeding rates. Line shows the least significant difference (l.s.d.). The model draws on data collected at 23 broods produced by 19 pairs.

focal watch, and the territory type also had no effect on female delivery rates (Table 1).

Male delivery rates also increased with nestling age and were higher in 1996 than in 1997 or 1998 (Table 1). However, in contrast to female thornbills, male delivery rates were related to their age and pair status (Table 1). This relationship was driven more by pair status than male age since older males in established pairs had higher delivery rates than both yearling and older males in new pairs (Fig. 2b). Male delivery rates were not affected by the sex ratio of the brood (Fig 2b, Table 1). The hatch date of the brood, the time of the focal watch, and the territory type also had no affect on male delivery rates (Table 1).

Sex ratio variation in the brown thornbill

The overall sex ratio of the 280 nestlings sampled (109 clutches, 48 females) was 53.2 % male. The sex ratio of the 215 nestlings from clutches where the sex of every egg was known (72 clutches, 41 females) was 54.4 % male. Neither of these sex ratios differ from parity (binomial tests, both $p > 0.5$).

The sex ratio of broods where the sex of every egg was known did not differ from the sex ratio of broods where one or more eggs were not sampled (GLMM model predictions: entire clutch sampled = 0.54 ± 0.04, part clutch sampled = 0.49 ± 0.07; Table 2). I therefore did not exclude partially sampled clutches from subsequent analyses. Brood sex ratios did not vary significantly between years (GLMM model predictions for brood sex ratio: 1995 = 0.57 ± 0.08, 1996 = 0.59 ± 0.07, 1997 = 0.47 ± 0.06, 1998 = 0.52 ± 0.06; Table 2), across the breeding season (Table 2), or between territory types (GLMM model predictions for brood sex ratio: natural woodland = 0.55 ± 0.05, watered plantation = 0.52 ± 0.05; Table 2). Brood sex ratios were also unrelated to the body size of either females or males (Table 2).

Brood sex ratios did vary significantly with "age and pair-bond duration" (Table 2). This relationship was driven principally by differences associated with pair-bond duration and not male or female age since established pairs produced

Table 2. Summary of analysis examining sex ratio variation in brown thornbill broods, modelled using the GLMM procedure. Female was specified as a random term in the mixed model, and the Wald statistics are reported for each term when entered in the model either alone or after controlling for the effect of pair-bond duration. For clarity of presentation, P values are only reported if they are below 0.1.

Explanatory variable	n	df	Single variable		With pair-bond duration	
			χ^2	P	χ^2	P
data quality	109	1	0.6	NS	0.3	NS
year	109	3	2.5	NS	0.9	NS
hatch date	109	1	0.2	NS	0.1	NS
territory type	109	1	0.4	NS	2.2	NS
female body size	105	1	0.0	NS	0.1	NS
male body size	104	1	0.5	NS	1.0	NS
age/pair-bond duration	69	4	12.1	< 0.05	-	
pair-bond duration	83	1	7.5	< 0.001	-	

male-biased broods whereas new pairs, regardless of the age composition of the pair, produced female-biased broods (Fig. 3). Pair-bond duration, alone, had a highly significant effect on brood sex ratio (GLMM model predictions for brood sex ratio: new pairs = 0.43 ± 0.05, established pairs = 0.65 ± 0.06; Table 2). Further, pair-bond duration tended to have a significant effect on brood sex ratio after controlling for both male and female age (pair-bond duration effect, $\chi^2_1 = 3.0$, $p = 0.08$), whereas neither male nor female age had a significant effect on brood sex ratio after controlling for the remaining two variable (male age effect, $\chi^2_1 = 0.5$, $p = 0.48$, female age effect, $\chi^2_1 = 0.1$, $p = 0.75$).

Experimental manipulation of brood sex ratio

All males increased their delivery rates as nestlings increased in age (age effect, $\chi^2_2 = 17.8$, $p = 0.0001$). Males in new pairs also tended to have lower delivery rates than males in established pairs (Fig 4a; pair status effect, $\chi^2_1 = 3.3$, $p = 0.07$), but neither the delivery rates of males in new pairs nor males in established pairs were affected by the sex of the brood (Fig. 4a: treatment effect, $\chi^2_1 = 1.4$, pair status.treatment interaction, $\chi^2_1 = 0.3$, both $p > 0.10$). Male delivery rates were also unrelated to the hatch date of the brood, the time of the focal watch, or the territory type (all $p > 0.25$).

All females increased their delivery rates as nestlings increased in age (age effect, $\chi^2_2 = 28.8$, $p < 0.0001$). Females, in both new and established pairs, also made more deliveries to male broods than female broods, although females in new pairs were more affected by the sex of the brood than females in established pairs (Fig 4b, pair status.treatment interaction, $\chi^2_1 = 11.9$, $p = 0.0005$). Female delivery rates were unrelated to the hatch date of the brood, the time of the focal watch, or the territory type (all $p > 0.25$).

The condition of nestlings in all-male broods provisioned by new pairs tended to decline more than the condition of nestlings in other experimental broods provisioned by either new or established pairs (Fig. 5; pair status.treatment interaction, $\chi^2_1 = 2.7$, $p = 0.1$). Changes in nestling condition were not affected by

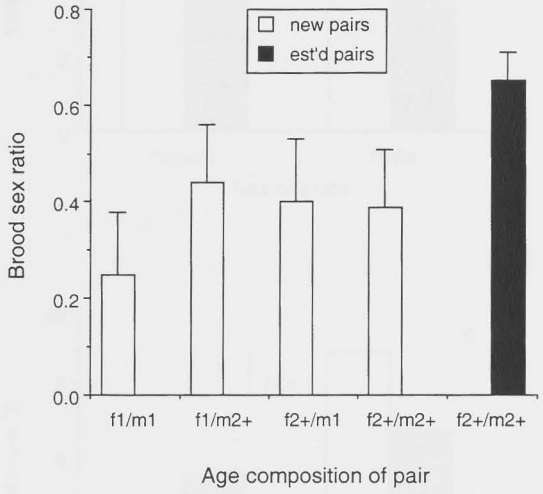

Figure 3. Relationship between the age composition and level of breeding experience shared by a pair and the sex ratio of broods produced by female brown thornbills. Bars show GLMM model predictions + S.E. New pairs are represented by stippled bars, and established pairs by the filled bar. The model draws on data from 69 broods produced by 43 females.

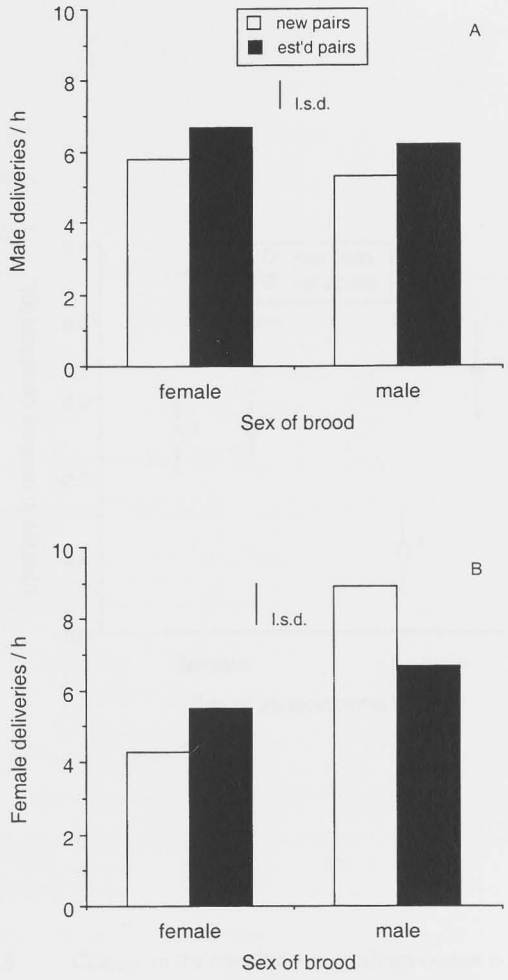

Figure 4. Relationship between the sex of a brood provisioned by new (open bars) and established pairs (filled bars) and the feeding rates of a) male thornbills and b) female thornbills. Bars show REML model predictions for 12 day old nestlings. Line shows the least significant difference (l.s.d.).

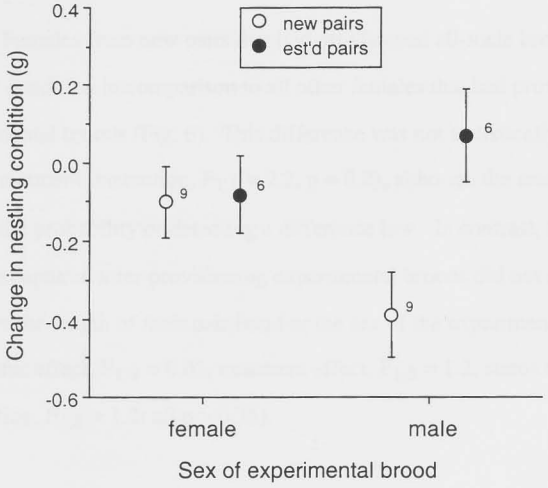

Figure 5 Change in the condition of nestlings (mean ± S.E.) between 7 and 11 days of age when fed by new (open circles) and established pairs (filled circle) in relation to the sex of the experimental brood. New pairs fed three all-male and three all-female broods, established pairs fed two all-male and two all-female broods.

hatch date, or territory type (both $p > 0.10$). The change in condition of foster chicks was also no different to the change in condition of biological chicks (chick type effect, $\chi^2_1 = 0.10$, $p = 0.75$). The latter result was confirmed with a within brood comparison of foster and biological chicks (change in condition of foster –change in condition of biological chicks: mean ± s.e. = 0.10 g ± 0.11, $t_9 = 1.30$, $p = 0.23$).

Females from new pairs that had provisioned all-male broods appeared to be in poor condition in comparison to all other females that had provisioned experimental broods (Fig. 6). This difference was not statistically significant (pair status.treatment interaction, $F_{1,8} = 2.2$, $p = 0.2$), although the small sample size makes the probability of detecting a difference low. In contrast, the condition of the 8 males captured after provisioning experimental broods did not appear to be related to either the length of their pair-bond or the sex of the experimental brood (Fig 6; pair status effect, $F_{1,8} = 0.01$, treatment effect, $F_{1,8} = 1.2$, status.treatment interaction, $F_{1,8} = 1.2$; all $p > 0.25$).

Discussion

The sex ratio of brown thornbill broods depended on the level of breeding experience shared by a pair. Female thornbills in new pairs produced female-biased broods while females in established pairs produced male-biased broods. Experimental evidence suggests that this pattern was adaptive because although sons have higher energy requirements than daughters the increased costs of raising sons are confined to females in new pairs. The costs of raising sons differ for females in new and established pairs because males in new pairs provision at a lower rate than males in established pairs and male thornbills do not adjust their feeding rates in response to the sex ratio of the brood. Females in new pairs with male-biased broods are therefore forced to provision at a higher rate and yet still produce nestlings that are in relatively poor condition and consequently unlikely to obtain a breeding vacancy.

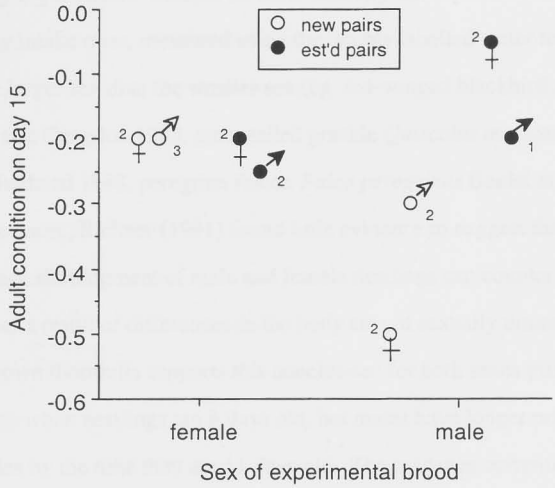

Figure 6. Condition of adults in new (open circles) and established pairs (filled circles) when nestlings were 15 days old in relation to the sex of the experimental brood they had been provisioning for 8 days. Numbers adjacent to the female and male symbols refer to the number of adults captured.

Provisioning behaviour of brown thornbills

Male-biased brown thornbill broods received more food from their parents than female-biased broods throughout the nestling period. This pattern may arise because male nestlings grow at a faster rate and reach a higher asymptotic mass than female nestlings in the brown thornbill (Chapter 4) and consequently have a higher energy requirement. Studies on other sexually dimorphic birds have found that energy intake rates, measured using the doubly labelled water technique, are higher in the larger sex than the smaller sex (eg. red-winged blackbird *Agelaius pheoeniceus* Fiala and Congdon 1983, great-tailed grackle *Quiscalus mexicanus* Teather and Weatherhead 1988, peregrine falcon *Falco peregrinus* Boulet et al. in press). Furthermore, Richner (1991) found little evidence to suggest that differences in the plumage development of male and female nestlings can counter the costs expected to arise as a result of differences in the body size of sexually dimorphic species. Data for brown thornbills supports this conclusion: for both sexes primary feathers start to emerge when nestlings are 8 days old, but males have longer primary feathers than females by the time they are 11 days old. The evidence currently available is therefore all consistent with the assumption that sons are more energetically expensive to raise than daughters in the brown thornbill.

The sex ratio of the brood had a different effect on the provisioning behaviour of male and female brown thornbills. Male feeding rates did not vary with sex ratio in either natural or experimental broods, whereas female thornbills consistently fed male-biased broods more than female-biased broods. This result is unusual since other studies on sexually dimorphic birds with sex-biased provisioning have found that either both parents or only male parents provision male-biased broods more than female-biased broods (eg. red-winged blackbird Yasukawa et al. 1990, oriental reed warbler *Acrocephalus orientalis* Nishiumi et al. 1996, great reed warbler *A. arundinaceus* Westerdahl et al. 2000). It is unclear why male thornbills do not adjust their feeding rate in response to the sex ratio of their brood but do feed at different rates when in new and established pairs. One plausible explanation is that male thornbills trade-off the time required to adjust their delivery rates rate to small

differences in demand associated with biased sex ratios for time spent detecting predators or in territory defence. I had the impression, although it was not measured quantitatively, that male thornbills were more likely to give alarm calls near the nest than females. Male thornbills may therefore decide on their feeding given the age of their brood and time constraints imposed by the status of their pair-bond, while female thornbills adjust their delivery to the actual demands of the broods. More detailed observations of begging behaviour are required to determine whether biased provisioning by female thornbills results from sex differences in nestling behaviour or adaptive female preferences for males.

Sex ratio variation in the brown thornbill

Sex allocation theory predicts that individuals should adjust the sex ratio of their brood in response to resource availability in order to maximise their reproductive success. I found that female thornbills in new pairs have mates that provision at a lower rate than females in established pairs and as predicted by theory produce female-biased broods, whereas females in established pairs, that have access to more resources, produce male-biased broods. Biased brood sex ratios may occur because females adjust their primary sex ratio (the sex ratio at fertilisation) or as a result of selective mortality of one or other sex between laying and fledging. In this study excluding broods where the sex of one or more eggs in a clutch was unknown does not alter the conclusions of my analysis. Furthermore, partial brood loss is extremely rare in brown thornbills (5 cases in 109 broods) and nestlings have never been observed to die as a result of starvation. My data therefore suggest that female brown thornbills produce broods with biased sex ratios by manipulating their primary, rather than secondary, sex ratio. Other studies also suggest that female birds may adjust their primary sex ratio in response to resource availability in order to maximise their fitness (Wiebe and Bortolotti 1992, Appleby et al. 1997, Komdeur et al. 1997, Nishiumi 1998, Westerdahl et al. 2000). Resource availability may be determined either by environmental conditions or by social conditions at the time of breeding. For example, Appleby et al. (1997) showed that the primary sex ratio

within tawny owl broods was related to vole densities on the breeding territory, and that broods contained more females (the larger sex) when vole densities were high. This pattern appears likely to be adaptive because the subsequent reproductive success of females, but not males, was dependent on the density of voles in the territory on which they were raised as chicks. In contrast, Nishiumi et al. (1996) showed that the level of resources available to female oriental reed warblers was dependent on their mating status since primary females were assisted by their mate but secondary females provisioned nestlings alone. Primary females were subsequently found to produce male-biased broods whereas secondary females produced female-biased broods (Nishiumi 1998). Female oriental reed warblers were argued to benefit from adjusting their primary sex ratio in response to their mating status because food supply was expected to have a stronger influence on the subsequent reproductive value of sons than daughters in this polygynous species. Neither study however evaluated the fitness consequences of the observed sex ratio biases experimentally.

This study adds to the growing body of experimental evidence (eg. Komdeur et al. 1997, Komdeur 1998, Nager et al. 1999, 2000) which suggests that sex ratio biases observed in a wild bird population are associated with significant fitness benefits for parents and young. Three results suggest that female brown thornbills in new pairs benefit from producing female-biased broods. First, females in new pairs have to feed at a far higher rate when provisioning all-male broods than all-female broods. Second, although females in new pairs are sensitive to the increased demand associated with provisioning sons they do not fully compensate for the low feeding rates of their mates. The condition of nestlings in all-male broods provisioned by new pairs declined more than the condition of nestlings in other experimental broods. Nestling mass prior to fledging has a significant effect on juvenile survival and subsequent recruitment in both male and female brown thornbills (Chapter 4). Third, females in new pairs that were provisioning all-male broods and had elevated feeding rates had lower condition scores than other adults captured while feeding experimental broods. Unfortunately, I was unable to determine if adult condition had

an effect on overwinter survival as an epidemic at the end of the 1998 breeding season resulted in the sudden mortality of 48% of the study population (Chapter 2). Nevertheless, considered together these results suggest that there are high fitness costs to females in new pairs associated with the production of male-biased broods as they have to work harder to provision them yet still produce sons that are in relatively poor condition and consequently less likely to obtain a breeding vacancy. In contrast, our results suggest females in established pairs are able to raise sons that are in good condition without paying a significant reproductive cost because their mates provision at a higher rate than males in new pairs. The extent to which females in established pairs benefit from producing male-biased broods rather than female-biased broods is unclear since precise information on the relative fitness benefits of well-fed sons and daughters is not available. However, the reproductive value of a well-fed son is likely to be higher than that of a well-fed daughter because nestling mass appears to have a greater effect on the recruitment of males than females (Chapter 4). Female thornbills therefore appear to obtain significant fitness benefits from adjusting the sex ratio of their brood in response to the level of resources provided by their partner.

A few studies suggest that female birds may also adjust the sex ratio of their brood in response to parental traits associated with paternal attractiveness (Sheldon 1998). For example, female collared flycatchers adjust the sex ratio of their brood in response to the size of their mates white forehead patch, a heritable trait associated with female choice, producing male-biased broods when paired to attractive males with large forehead patches (Ellegren et al. 1996). However, I found no evidence that female brown thornbills adjusted the sex ratio of their brood in response to either their own body size or the body size of their mate as was predicted given that body size may influence the attractiveness of sons in this species. This may be because extra-pair paternity is rare in the brown thornbill (Chapter 5), and body size therefore does not have a large effect on the relative reproductive value of sons and daughters.

Recent studies have demonstrated that chromosomal sex determination does not always prevent adaptive manipulation of the primary sex ratio in birds. Extreme

sex ratio biases have been observed in Seychelles warbler where females without helpers on high and low quality territories produced 13% and 77% sons, respectively (Komdeur et al. 1997). The magnitude of the sex ratio bias observed in the brown thornbill (new pairs = 43% sons, established pairs = 65% sons) is more typical of observed sex ratio biases in other wild bird populations (eg. Nishiumi 1998, Westerdahl et al. 2000). However, there are also several studies, based on large sample sizes, where no adaptive skews in sex ratio can be detected (eg. Radford and Blakey 2000). Further studies are obviously required to determine the extent to which diverse selection pressures have led to the evolution of mechanisms that allow control over sex ratio in birds.

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Chapter 7

Pair-breeding in the Acanthizidae: synthesis and future directions

My work has demonstrated that brown thornbills breed exclusively in pairs and that young brown thornbills, even when they have the opportunity, never help their parents to raise siblings from subsequent broods (Chapter 2). Since pair-breeding is a derived trait in the Acanthizidae (Nicholls et al. 2000), brown thornbills provide a rare opportunity to evaluate explanations for the evolution of pair-breeding in birds.

If pair-breeding has evolved from cooperative breeding in response to the relaxation of ecological constraints on dispersal and independent reproduction we might expect that pair-breeding is associated with a reduction in either the costs of dispersal to suitable habitat or the benefits of natal philopatry. However, I found no evidence that pair-breeding can be explained by reversing the argument generally used to explain cooperative breeding. Pair breeding and cooperative species in the Acanthizidae are all sedentary, have low annual mortality, and produce modest numbers of young that will have few opportunities to disperse to a breeding vacancy (Chapter 2). Under these circumstances juveniles of both pair-breeding and cooperative species may benefit from prolonged natal philopatry. There are benefits to delayed dispersal in both pair-breeding and cooperative species of Acanthizidae (eg. brown thornbills Chapter 4, white-browed scrubwrens *Sericornis frontalis* Leedman 2000). Juvenile brown thornbills that delayed dispersal were four times as likely to recruit into the breeding population.

However, despite the advantages of delayed dispersal, I found that only 54% of brown thornbill pairs that raised one or more son to independence retained a son on their territory. Constraints on delayed dispersal reduce opportunities for cooperation because the majority (72%) of the juvenile males that remained on their natal territory were able to either move to a local vacancy or bud off a territory and attract a mate by the start of the following breeding season. Consequently, only a small number of the juvenile males that delayed dispersal had the opportunity to help their parents (4 cases in four years). Potential helpers were all one year-old-males and may not have helped because they are more likely to reduce, rather than enhance, their parents' reproductive success. I found one-year-old male thornbills had

extremely low reproductive success when breeding independently because they were more likely than older birds to attract predators when provisioning nestlings (Chapter 3). The critical question in attempting to explain the evolution of pair-breeding in brown thornbills is therefore, why more juvenile thornbills do not postpone dispersal and remain on their natal territory?

What constrains prolonged natal philopatry?

There are two hypotheses that could explain why more juvenile brown thornbills do not delay dispersal when there appear to be large benefits associated with prolonged natal philopatry. First, competition between parents and offspring over opportunities to reproduce may reduce the future reproductive success of adults sufficiently that parents obtain fitness benefits from evicting young when they reach independence (Cockburn 1996). Second, the food supply on the permanent territories occupied by the breeding pair may often be insufficient to support an extended family during the non-breeding season (Rowley 1968, Koenig et al. 1992). The costs and benefits to adults and juveniles of prolonged natal philopatry will then determine whether juveniles disperse of their own volition or are forced to leave by parental aggression.

Does reproductive conflict limit delayed dispersal?

Competition between parents and young over the opportunity to reproduce in brown thornbills may significantly reduce the fitness of parents in two ways. First, juveniles that do not disperse may acquire part of their natal territory and attempt to breed independently. This will reduce the level of resources parents have for subsequent breeding attempts and may reduce their future reproductive success. Alternatively, sons that do not disperse may compete directly with their fathers for paternity in subsequent broods.

I found that pairs that allowed sons to remain on their natal territory also frequently (12 of 25 cases) conceded part of their territory to their son at the start of the following breeding season. Territory size in the brown thornbill appears to

depend on food supply. Bell and Ford (1986) found that while territories varied in size they all contained approximately the same amount of shrubs, which suggests that food availability may be similar on all territories. Further, I found that watered territories, that are likely to be buffered against seasonal declines in food availability, were significantly smaller than territories in natural woodland (Chapter 2). Parents that lose part of their territory will therefore have access to fewer resources, which may significantly reduce their future reproductive success.

The possibility that sons that are not forced to disperse may compete with their fathers over paternity in subsequent breeding attempts may be evaluated indirectly by comparing patterns of paternity loss in members of the Acanthizidae. Paternity studies on cooperative species in this family suggest that dominant males that breed in groups are unlikely to lose more paternity than dominant males that breed in pairs (Table 1). Furthermore, levels of extra-pair paternity in all three *Acanthiza* species that have been studied to date are low. Competition between fathers and sons over paternity is therefore unlikely to lead to conflicts of interest about the timing dispersal.

My data suggest that there may be some cost to adults of allowing juveniles to remain on their natal territory. However, I found no evidence that dispersal was prompted by parental aggression. Parental aggression has been observed to lead to dispersal in other species from the Corvida (eg. white-throated treecreeper *Cormobates leucophaea* Noske 1991, superb fairy-wren *Malurus cyaneus* Mulder 1995). If there were conflict over the timing of dispersal in brown thornbills then parental aggression would likely have been observed. The costs to adults of juvenile retention therefore appear to be outweighed by the benefits they obtain by promoting the survival and recruitment of their offspring. Nevertheless, further study aimed at determining how sons obtain part of their natal territory is necessary in order to determine whether parents are always willing to concede part of their territory to their offspring.

Table 1. Paternity loss (% nestlings, N) by dominant males in pair-breeding and cooperatively breeding species from the Acanthizidae.

	Pairs	Groups		
		Total	Subordinates	Extra-group
Brown thornbill[1]	6.2% (178)			
Buff-rumped thornbill[2]	1.4% (70)	6.8% (44)	2.3%	4.5%
Yellow-rumped thornbill[2]	4.5% (88)	4.8% (21)	4.5%	0
White-browed scrubwren[3]	24.0% (50)	24.1% (87)	18.4%	5.7%

([1] this study; [2] D. Ebert personal communication; [3] Whittingham et al. 1997)

Does food supply limit opportunities for delayed dispersal?

Sympatric species of Acanthizidae partition resources by foraging at different heights and having preferences for different foraging substrates (Recher 1989). Brown thornbills feed principally on invertebrates gleaned from the foliage of shrubs, whereas cooperative species in the family prefer to feed on invertebrates found on eucalypt foliage, grass, or leaf litter (Recher 1989, Bell and Ford 1990, Magrath et al. 2000). Could differences in invertebrate abundance in the microhabitats used by members of the Acanthizidae explain interspecific differences in the number of juveniles that postpone dispersal and remain on their natal territory? Several species of insectivorous passerine in Australia typically forage more on the ground in winter than in summer, suggesting that foraging on foliage is less profitable in winter compared to other seasons (Cale 1994, Ford et al. 1990). Further, eucalypt species produce new foliage more or less constantly throughout the year (Florence 1981), and as a result there is little seasonal fluctuation in invertebrate abundance on eucalypt foliage (Woinarski 1985). Little is known about seasonal growth patterns in Australian shrubs, but if growth is more seasonal brown thornbills, a specialist shrub forager, may experience more marked seasonal lows in invertebrate abundance than the cooperative species that forage in the canopy, on the ground, or in the leaf litter.

The hypothesis that food supply constrains the number of juvenile brown thornbills that may postpone dispersal is hard to evaluate using observational data. I found that sons on watered territories were no more likely to delay dispersal than sons on territories in natural woodlands, but this is not necessarily inconsistent with the hypothesis as there may be little variation in food supply between territories as territories in good habitats are smaller. Similarly, over the four years of the study the majority of territories (79%, n = 24 territories that produced sons) had a juvenile male delay dispersal in one or more years. Again this may not be inconsistent with the hypothesis that food supply influences dispersal if retention of a son in one year depress food resources and the likelihood a son can delay dispersal in the next. Experiments that both manipulate food resources by changing shrub cover, and

increase overall productivity by protecting nests from predators, are required to test if differences in resource availability on territories influence the timing of dispersal in thornbills.

Benefits of philopatry and conflicts of interest between siblings

The probability that juvenile males are able to recruit into the breeding population is strongly correlated with the timing of dispersal. The ability of males to delay dispersal and obtain the benefits of natal philopatry is therefore likely to be influenced not only by resource levels on the territory, but also by interactions with their siblings. For example, dominant brood members have been reported to expel subordinate siblings from their natal territory in the grey jay *Perisoreus canadensis* (Strickland 1991). I found little evidence to suggest that older or larger males were more likely to delay dispersal than their smaller or younger siblings. However, the sample size was limited. Further study is therefore required to examine the role of intra-brood dominance on dispersal strategies and recruitment in brown thornbills.

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